



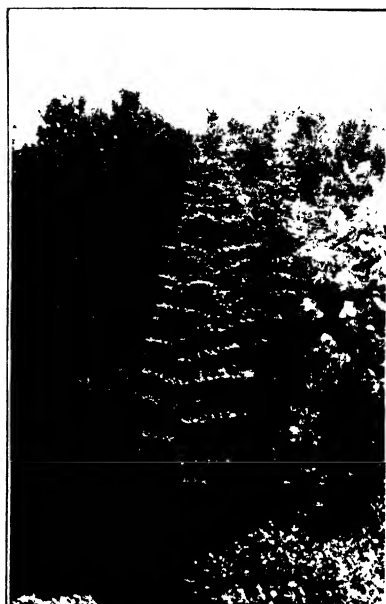
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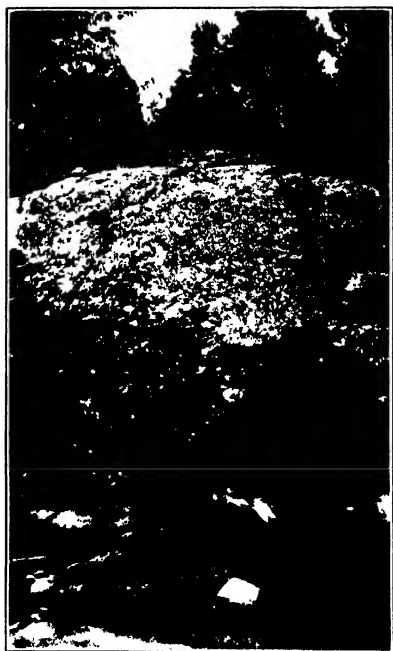
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A



B



C



D

PLATE I. A. Recent burn on southwest end of Smithwick Island. Picture taken in 1909, five years after fire. B. Picture taken in 1926, from same point as A. C. Shore rocks at Rock Harbor Lodge in 1909. D. The same in 1926.

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SEVENTEEN YEARS OF SUCCESSIONAL CHANGE UPON ISLE ROYALE, LAKE SUPERIOR

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At the present time we have attained to a considerable knowledge of the manner of succession and the causes thereof; a large quantity of facts has been accumulated, and a number of generalizations and laws have been formulated. One phase of the subject remains still obscure: the *rate* of successional change. Data pertaining to this are not easy to obtain. Historical records occasionally provide valuable facts, but the finding of such is usually a mere fortunate accident. Periodic observation of selected localities is the only dependable method, and so far such studies have been rare. One naturally hesitates before expending much time upon the making of careful surveys and the establishment of permanent quadrats, knowing that a period of five or ten or twenty years must elapse before the fruits of one's labor may be gathered in. Nevertheless the results are so valuable, for both science and practice, that long-period studies ought to be initiated wherever possible. In the meantime, in view of the present dearth of recorded facts, any observations bearing upon this subject must be welcomed, even though limited in scope and insufficient to justify any sort of generalization.

In 1909 and 1910 I carried out an investigation of the vegetational successions upon Isle Royale, in Lake Superior, in the course of which I made many photographs and laid out a number of quadrats.¹ Having no thought of future visits, I allowed the locations of these to remain unrecorded. When in 1926 an opportunity to revisit the island presented itself I found my natural desire to learn something of the successional changes that had occurred in the interval sadly hampered by this neglect. I succeeded, however, in locat-

¹ The successional processes upon Isle Royale are described in the following papers by the present writer:

The ecological succession of mosses, as illustrated upon Isle Royale, Lake Superior. *Plant World*, 15: 197-213, 1912.

The climax forest of Isle Royale, Lake Superior, and its development. *Bot. Gaz.*, 55: 1-44; 115-140; 189-235, 1913.

ing the positions from which a number of important pictures were made on my earlier visits, and a comparison of the pairs thus obtained reveals facts that are decidedly worth putting on record. All the earlier photographs here used were made in 1909, so that the interval is in every case seventeen years.

The most rapid rate of change was found to have taken place, as was expected, in the secondary Burn Succession. The locality studied is Smithwick Island, one of the row bounding Rock Harbor on the southeast, and nearly opposite Rock Harbor Lodge. The substratum is smoothly glaciated lava of Keweenawan age, with a thick layer of purely organic soil resting upon it, the accumulation from many centuries of forest growth. The virgin forest is typical climax of balsam fir (*Abies balsamea*), white spruce (*Picea canadensis*) and paper birch (*Betula alba* var. *papyrifera*). In the year 1904 (or possibly 1903) the southwest end of the island suffered a severe burn, which almost completely destroyed the forest trees; only here and there a birch survived. It was in the main a slow fire, eating through the dry peat and undermining the trees, which fell and were consumed where they lay. The organic soil was burned from the higher and drier rocky areas, but in the depressions it suffered much less harm.

In 1909 the burned area appeared as in Plate IA. The greater portion was thickly covered by species commonly associated with such conditions. The two most abundant were pearly everlasting (*Anaphalis margaritacea*) and fireweed (*Epilobium angustifolium*); next in importance were red-top (*Calamagrostis canadensis*) and red raspberry (*Rubus idaeus* var. *aculeatissimus*). In the depressions a considerable amount of forest vegetation had survived: two-leaved Solomon's seal (*Maianthemum canadense*), bunchberry (*Cornus canadensis*), twin-flower (*Linnaea borealis* var. *americana*), shield-fern (*Aspidium spinulosum*), ground pine (*Lycopodium annotinum*). A few forest shrubs persisted also: mountain maple (*Acer spicatum*), high-bush cranberry (*Viburnum pauciflorum*) and even ground hemlock (*Taxus canadensis*). Very occasional seedlings of balsam and white spruce were found, and birch and mountain ash (*Pyrus americana*) showed the beginnings of stump sprouting.

A quadrat 25 ft. square supported the following population:

<i>Epilobium angustifolium</i>	806
<i>Anaphalis margaritacea</i>	421
<i>Maianthemum canadense</i>	312
<i>Betula papyrifera</i> (sprouts)	117

It was found in 1926 that the advance during the interval of seventeen years had been far from uniform over the area of the burn. Some portions still supported a dense growth of fireweeds, although even here young balsams and birches were in evidence. Other areas, which in 1909 were densely covered with fireweeds, were now rather heavily shaded by birches and balsams,

some of them twenty five feet tall. A thin layer of humus covered the rock fragments beneath the trees, and a copious growth of forest herbs and shrubs had developed, among which were found frequent relict individuals of *Epilobium* bearing large pale leaves.

A and *B* of Plate I demonstrate the development during seventeen years in an area of maximum rapidity of change. The relict birch has fallen, its overturned stump being visible in the lower left corner of the second picture. The rapid growth of young birches and balsams has wrought a complete change in the landscape.

Increment borings of nineteen balsams within the field of the photograph, made so close to the ground that the count almost certainly gives the true age of the tree, provided the following results. Five trees entered during the years 1901 to 1903, thus antedating the fire and surviving because of the comparative moistness of the soil in this particular spot. Of the fourteen individuals that have come in since the fire, ten started growth within four years after it—two in 1905, five in 1907 and three in 1908. All of these ten and the five that entered before the fire were therefore in existence at the time of the first photograph, but were hidden by the rank growth of fire-weeds. It is also of interest to note that the average width of ring in the pre-fire individuals, .119 inch, was more than twice as great as in the post-fire group, in which it was .051 inch.

Passing to the Rock Shore Succession, we find in the rock surface phase of that series the opposite extreme in rate of change. Crustose and foliose lichens are notoriously slow of growth, but it was rather surprising to discover, so far as the photographic method is capable of recording, almost no indication of change whatsoever. The two pairs of pictures, Figure 1, *A* and *B* and Plate I, *C* and *D*, exhibit shore rocks of the prevalent Keweenaw lava at Rock Harbor Lodge. A careful examination of Figure 1 reveals the fact that each and every lichen thallus appearing in 1909 is exactly duplicated in 1926. Nowhere is there evident change in size or shape; no new patches can be discovered and none has disappeared. *C* and *D* of Plate I show a slightly later stage in development, with foliose lichens and xeric mosses (mostly *Grimmia ovata*) sharing dominance. Here, too, we find practically no evidence of change. It is just possible that certain of the moss patches in the lower right portion have extended themselves very slightly.²

² Mr. Louis H. Powell, of the Department of Geology, University of Minnesota, reports an interesting case similar to those here given. He writes as follows: "It is common on all of the travelled routes in northern Canada to see initials of Indians and the dates of their visits along with rude sketches chipped on the lichen-covered, glacier-polished rock outcrops. The figures and letters stand out bare and distinct for years." He further states that in June, 1927, he found such a date upon a polished granite cliff in front of the Hudson's Bay Company's post at Norway House, at the north end of Lake Winnipeg. It had been marked by chipping away the orange crustose lichens from the rock surface to form the figures. The rock exposed by the removal of the lichens had darkened, but the figures could be fairly easily distinguished, and the date of marking was either 1894 or 1896. The lichen was probably a species of *Placodium*.

In the crevice phase of the Rock Shore Succession, seventeen years' time has brought progress, not great in amount, but nevertheless distinct. In plate II *A*, taken in 1909, no shrubs are visible; my field notes record "in



A



B

FIG. 1. A. Shore rocks at Rock Harbor Lodge in 1909. B. The same in 1926.

rather sheltered places very stunted clumps of *Sorbus* [*Pyrus americana*]." The photograph of 1926 (Plate II, *B*) shows a number of conspicuous bushes of that species: "about eight clumps, maximum six feet high." In another locality, upon one of the northwest-facing cliffs characteristic of Isle Royale, (Plate II, *C* and *D*) progress was evident in the increase in size of trees growing in crevices (mostly balsams and birches) and in the establishment of new individuals. The proportion of the cliff surface hidden by vegetation is manifestly greater, and, incidentally, the forest crowning the cliff is distinctly more compact. These observations upon the two phases of the Rock Shore Succession confirm the impression that progress toward the climax depends largely upon the plants rooted in the crevices.

Observations upon the Bog Succession were inconclusive, due to indistinct-



A



B



C



D

PLATE II. A. Islets near Rock Harbor Lodge in 1909. B. The same in 1926. C. Cliff on islet near Rock Harbor Lodge in 1909. D. The same in 1926.

ness of vegetational boundaries and lack of satisfactory landmarks. One fact is worth noting: the recent arrival of moose upon the island, followed by their rapid increase, has resulted in the conversion of the sedge mat zone in many of the bog localities to a mere mud wallow.

Generalizations from such scanty data are inadvisable, but yet a moral may be drawn. In visiting a new region for the purpose of ecological study one is apt to take it for granted that the first visit will be also the last. Photographs are made and quadrats staked out, but the localities thereof are usually left unmarked and unrecorded. Why not rather assume a future return, and mark the locations of important photographs and make every quadrat a permanent one? The very initiation of such a program will tend to draw the founder back to his work and there is the chance, too, that, if the localities are accurately put on record in printed form, some other worker may have the opportunity to visit the scene and carry on the study.

SOIL CHANGES AND SILVICULTURE ON THE HARVARD FOREST

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Since its establishment in 1908, the Harvard Forest has dealt primarily with a type peculiarly characteristic of central New England, and one which, on account of marketability and apparent productiveness, has been taken as the chief objective in the development of regional forestry—the white pine (*Pinus strobus* L.) stands that seeded in on thousands of acres of farm land abandoned during the middle and latter part of the last century. In addition to this—the prevailing type—the Forest contains stands representing two other kinds of origin: first, several small areas of virgin forest, uneven-aged hardwood mixed with hemlock (*Tsuga canadensis* (L.) Carrière) and some white pine; and second, blocks of even-aged second growth, either hardwood or mixed hardwood and pine, which originated from the clear cutting of the virgin stand.

With these examples of varying life histories for comparison, it early became apparent that white pine in pure stands was a transition type, or intermediate stage in the succession, and one not in the long run suited to the comparatively heavy soils of the region. Always containing a variable admixture of hardwood, these forests develop in later life not an advance growth of pine, but one of broad-leaved species, such as white ash (*Fraxinus americana* L.), red oak (*Quercus borealis* Michx., formerly designated *Q. rubra* L.), sugar maple (*Acer saccharum* Marshall), black and yellow birch (*Betula lenta* L. and *B. lutea* Michx.), red maple (*Acer rubrum* L.), etc. This advance growth is not only a serious obstacle to the reproduction of the pine by any method of cutting, but an index of a strong tendency toward reversion to the original, or virgin, type. On the other hand, the pine stands themselves do not exhibit a satisfactory condition. They prune themselves slowly, seldom produce any but low grade lumber, and at the age of 50 to 60 years almost always show a sudden decline in growth, together with increasing evidence of ill health. Both prolonged observation, as well as systematic studies of stand development (Harvard Forest bulletins 7 and 8), have established the conviction that the conversion of the old field white pine type into mixed stands is, on the score of productiveness, quality, and cost of formation, the best policy.

Thus, the annual cuttings in the white pine type have had for their object either the formation of a mixed stand of the best hardwood species or a

mixture of hardwood and white pine. On areas where the advance growth of ash, oak, etc., is sufficiently abundant, the operation consists merely in one clean cutting of the stand, accompanied by complete disposal of limb wood and slash, either for fuel wood or by burning. In cases where the advance growth is less abundant or satisfactory, an admixture of white pine reproduction has been secured by one preparatory or seed cutting, followed after four to six years by the removal of the remaining stand. Or, if natural reproduction seems unlikely on account of an unfavorable seed bed, a clear cutting is followed by the planting of pine in groups or small patches where the soil is favorable and hardwood advance growth is scanty. Thus in some operations the previous stand is removed at once, and in others it is taken off in two cuts from four to six years apart. In both cases the subsequent conditions and treatment of the reproduction area are alike.

After the final removal cutting there follow from two to four years when the ground is more or less exposed to the sun and the elements. This exposure, however, diminishes very rapidly with the successive development of several strongly marked phases of vegetation. In the second year a dense growth of hay-scented fern (*Dicksonia punctilobula* (Michx.) Gray) with annual weeds and some grasses nearly covers the surface. In the third year *Rubus*, particularly high bush blackberry (probably *R. allegheniensis* Porter) and raspberry (*R. ilaens* L.) of very strong development, often dominates the ferns and lower vegetation. Meanwhile the hardwood seedlings and seedling sprouts have reached a height of four to eight feet. In the next eight years, two or three weedings or cleanings are applied, the object of which is the earliest possible closing of the cover compatible with desirable composition. This means in practice lopping only such weed trees or stump sprouts of too rapid growth as are likely to suppress the desirable species. Of the hardwoods, whether with pine groups in mixture or not, those chiefly favored are white ash, red oak, sugar maple, white birch (*Betula papyrifera* Marshall), yellow birch, beech (*Fagus grandifolia* Ehrh.), and basswood (*Tilia glabra* Ventenat, formerly designated *T. americana*). In from eight to ten years, depending somewhat on the soil and the density of the young growth, the new stand, now composed almost wholly of the favored species, has established a continuous canopy, which rapidly shades out the ground vegetation, not only most of the herbaceous species, but also *Rubus* and other low shrubs.

That this conversion of type has been accompanied by rapid and beneficial changes in soil condition has been abundantly evident, not only in the strong development of new vegetation following cuttings, but still more in the vigorous growth of the succeeding mixed stands. It is due to Dr. Henrik Hesselman, Director of the Swedish Institute of Experimental Forestry, who has lately visited the Harvard Forest, that these alterations in the soil profiles can here be identified and interpreted in more definite terms.

wood stand and two to three acres of the adjacent old field pine type, areas sufficient in size to eliminate the influence of lateral exposure.

The original pine stand, now approximately eighty years old, contains a scattered understory of hemlock and a few hardwoods, yellow birch, white ash, red maple and black cherry (*Prunus serotina* Ehrh.). The soil profile exhibits a distinctly podsolized horizon.¹ Beneath a thin layer of dry leaf litter, chiefly pine and hemlock needles, is a deep zone of duff, composed of raw humus, which merges into the characteristic leached layer. Below this is a thin burnt sienna or enriched stratum, which has remained apparently unchanged, both in depth and organic content, for many years. There is almost no ground cover. Scattered partridge berry (*Mitchella repens* L.), star flower (*Trientalis americana* (Pers.) Pursh.), and goldthread (*Coptis trifolia* (L.) Salisb.) are the chief species. Hardwood advance growth consists of stunted but fairly abundant seedlings of white ash, red oak, yellow birch and red maple. With an organic layer decomposing very slowly and of such depth as to exclude all but the heaviest rainfalls, it is plain that the soil is in a static condition and without active fertility.

Physiological and soil conditions in the young hardwood forest are in striking contrast to those in the original pine stand. The soil on this, as on other similar areas, was identified by Dr. Hesselman as a true mull profile, in which both the heavy litter and organic layer that had accumulated in the previous stand, as well as the current annual leaf fall, have been almost completely decomposed and merged with the mineral soil to a maximum depth of five or six inches. The resulting brown earth closely resembles the best garden loam in porosity, color, uniformity of texture, and moisture content. So active is the decomposition of litter that less than one year's leaf fall remains on the ground, and even this is so thin as to expose the mineral soil over nearly 25 per cent of the surface. Herbaceous ground cover is in general scanty and undersized. The prevailing species are hay-scented fern and a small white aster (*Aster acuminatus* Michx.). A significant factor is the change in the bird population. Instead of the black-throated green warbler (*Dendroica virens* Gmel.), hermit thrush (*Hylocichla guttata pallasii* Cab.) and oven bird (*Seiurus aurocapillus* L.) of the pine wood, the noticeable birds are now the wood thrush (*H. mustelinus* Gmel.), Maryland yellow throat (*Geothlypis trichas brachydactyla* Swain) and woodcock (*Philohela minor* Gmel.), the latter a notable feeder on earthworms. The hardwood stand as a whole is dense and exceptionally thrifty, now at eighteen years old from two to five inches in breast height diameter, and twenty-five to thirty feet in height. Nearly 50 per cent of the mixture is white ash, with red oak, sugar maple, white birch, yellow birch, and scattering basswood, black cherry and red maple making up the remainder. Natural pruning, especially with

¹ The matter of podsol soil will be discussed more fully in the April issue of *ECOLOGY*, Vol. IX, No. 2, by Paul W. Stickel in an article "Podsol Soil: Its Physical Characteristics and Silvicultural Importance. Ed.

ash, has proceeded so rapidly that dominant trees have lost their side branches to a height, in many cases, of twelve feet. The stand appears to combine the highest prospective quality with the maximum rate of growth.

The full interpretation of this striking transformation in vegetation and soil profiles, both as regards chemical and biological factors and practical control under wider variations of site and composition, must await more systematic study; but with so many stages of the conversion process now available on the Forest, there are a few observations and conclusions that may be made already.

The development of the mull profile is complete in from twelve to fifteen years after the removal of the pine.

The rate of development, granted uniform density in the new stand, is affected very little by minor variations in topography.

Given similar drainage, the mull is deepest under ash and sugar maple, less deep under white and yellow birch.

Whether the previous pine stand is removed at one cutting or by a thinning and final cutting six years apart, there is no substantial difference in the rate of soil change.

Extreme dryness or extreme wetness of soil, such as occurs on sharp knolls or in small swamps, appears to arrest decomposition, and therefore to perpetuate the original soil profile.

The debris left from weeding in the young stand, consisting sometimes of stems up to an inch and a half in diameter, has entirely disappeared in from six to ten years.

Small variations in the composition of the previous stand do not appear influential, but a mull horizon seems to develop faster after the cutting of a stand containing 25 per cent or more of hardwood.

Where pine groups up to two rods (10 meters) in diameter are included in the converted stand, the soil—at least after nineteen years—appears to be the same as under pure hardwoods.

In this experience with soil changes on the Harvard Forest, there is a lesson for silviculture. Podsolized soil, except possibly in northern regions where it may be unavoidable, indicates soil deterioration and relatively poor growing conditions. It develops commonly in pure white pine stands, which fall off in growth and health at comparatively short rotations. The mull soil, on the other hand, is fertile and active. It develops rapidly in mixed stands, which have long been recognized, even by lumber operators, to produce the largest and best quality of softwood timber. The natural tendencies of the present transition types in central New England are toward reversion to mixtures of species, which can usually be more cheaply established than pure stands of softwood. There are thus strong biological as well as economic reasons against the maintenance of pure white pine as a permanent type. Conversely, the formation of mixed types means good silviculture and sound business.



A. Original old field white pine stand (control area), now 80 years old.



B. Converted stand of mixed hardwoods 18 years after clear cutting the pine stand. Before cutting, this area looked like A above. Note large pine stumps.

SUMMARY

On comparatively heavy soils in central New England, forests of pure white pine (*Pinus Strobus*) develop on abandoned fields as an intermediate stage in succession. These forests, covering a large aggregate area, have been the chief objective in the regional forestry. They show, however, strong tendencies to revert to hardwood, rendering reproduction of pine difficult. They produce only low grade lumber, and decline rapidly in growth and vigor after 50 to 60 years of age.

The conversion of these forests to stands of the more valuable hardwoods, or mixtures of hardwoods and pine, can be accomplished by removing the pine in one or several cuttings, followed about four years later by cleanings or weedings to favor individuals of the desirable species.

The soil profile under a certain 80-year-old white pine stand with almost no ground cover shows a thin layer of dry needle litter, a thick layer of raw humus, and a strongly podsolized horizon, below which is a thin typical burnt sienna or enriched stratum. These conditions are unfavorable.

Under an adjacent 18-year-old hardwood forest, where the soil profile at the time the pine was removed resembled the present profile under the white pine, there is now a true mull profile. The rate of decomposition has become so rapid that not only has the accumulated raw humus merged with the mineral soil, but less than a single year's leaf fall now remains on the surface of the ground. The humus-enriched earth closely resembles the best garden loam in porosity, color, uniformity of texture, and moisture, and contains many earthworms.

The bird population has changed from the black-throated green warbler, hermit thrush and oven bird of the pine wood to other species among which the Maryland yellow throat and woodcock are noticeable.

The hardwood stand is dense, thrifty and growing rapidly.

On lands showing tendencies to hardwoods, mixed stands can be secured more cheaply than stands of pure pine, and, since they greatly improve soil conditions and show thrifty growth, they represent good silviculture and sound economics.

INFLUENCE OF ENVIRONMENTAL CONDITIONS ON THE ACTIVITIES OF CELLULOSE DECOMPOSING ORGANISMS IN THE SOIL

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INTRODUCTION AND HISTORICAL

It is known that the soil harbors a great variety of organisms capable of decomposing cellulose; numerous representatives are found among the fungi, actinomyces and bacteria. However, the isolation from the soil of an organism which is able to perform a certain reaction, is no proof that this organism takes an important part in this particular process under natural conditions. Although a considerable amount of work has been devoted to the description of all these groups of organisms which may decompose cellulose, quantitative data concerning their relative importance in nature are extremely meagre.

Waksman and Skinner ('26) observed a striking parallelism between cellulose decomposition in soil and increase in the numbers of fungi. They concluded therefrom that, in humid soils, fungi are largely responsible for the decomposition of cellulose. The plate method and, in some cases, the direct microscopic examination, were used to determine the abundance of the microorganisms. But as the authors pointed out themselves, the ordinary laboratory media, used by them for plating, probably did not allow for the development of cellulose decomposing bacteria if there were any present; this fact has been confirmed during the present work.

Concerning the part, played by the actinomyces, we have the observations made by Conn ('16) and Martin ('23) who noticed an increase in the number of actinomyces as a result of the decomposition of grasses and green manures. Since these crude organic materials contain so many substances besides cellulose, there is no proof that the increase in the numbers of actinomyces is due to the decomposition of the latter substance. As a matter of fact Waksman and Skinner ('26) could not observe any such increase following the addition of pure cellulose.

It is only on the basis of a number of qualitative tests that McBeth ('16) made the following statement: "In the humid soils of the East, the filamentous fungi are perhaps of greater importance than bacteria in the destruction of cellulose, while in the semi-arid soils of the West, the reverse is apparently true."

Waksman and Carey ('26) present some evidence pointing to the fact that, in normal soils, no anaerobic flora capable of decomposing cellulose is active. But such a flora, consisting of spore forming bacteria, becomes established after the soil has been kept for some time under water.

It has been the object of the present work to determine the relative activities of the different groups of organisms capable of decomposing cellulose under different sets of conditions.

EXPERIMENTAL

Methods

An attempt has been made to follow at the same time (*a*) the variation in the numbers of cellulose decomposing organisms under certain conditions, (*b*) the progress of cellulose decomposition under the same conditions, and to correlate these two sets of phenomena. These studies have been made first in sterilized soils inoculated with pure and mixed cultures; the results thus obtained were used for the interpretation of studies in normal soils.

The numbers of fungi and actinomyces were determined by the plate method, using respectively Waksman's ('22) fungus agar and starch agar as media. It is fully realized that the determination of the numbers of fungi may give results difficult of interpretation. The colonies developing on the plate may come from either a spore or a piece of mycelium, large or small. A young active mycelium may give rise to only few colonies, while at the stage of spore formation, the number of colonies will increase enormously beyond the proportional increase in actual cell growth. As a matter of fact, it has even been suggested that high numbers of fungi indicate spore formation, which may be associated with low activity of these organisms. But quantitative studies not reported here have demonstrated that, while there is no proportional relationship between "numbers of fungi" and "rate of cellulose decomposition" (even where fungi are known to be the only organisms active), there is no doubt that, if a soil shows a large increase in the numbers of fungi soon after the application of cellulose, we are justified in inferring that fungi play a part in the process.

The same considerations hold true in the case of actinomyces.

The numbers of cellulose decomposing bacteria have been determined by means of the dilution method outlined elsewhere.¹

The cellulose determinations were made by the method described by Charpentier and modified by Barthel and Bengtsson ('24).

The CO₂ evolution was measured in an aeration apparatus similar to the one described by Waksman and Starkey ('24).

It is recognized that the proportion of carbon given off as CO₂ from every unit of cellulose decomposed may vary greatly with the different organisms. But it has been established in studies not reported here that, in the case of

¹ To be published in the Journal of Bacteriology (1928).

impure cultures, about 50 to 60 per cent of carbon is given off as CO_2 , whether the cellulose is being decomposed by fungi, bacteria or actinomyces. The CO_2 evolution is therefore a satisfactory index of the rate of cellulose decomposition.

In all cases where nitrogen salts have been added to the soil in order to allow a rapid decomposition of the cellulose, they have been introduced in the proportion of one unit of nitrogen for each thirty units of cellulose.

1. *Studies in Liquid Media*.—Because of the peculiar physical and physico-chemical properties of the soil as a medium, studies in liquid media are of limited value for an interpretation of the activity of the organisms concerned in the different soil processes. The results of such studies must naturally be used only to elaborate upon studies in soils, and should in any case be interpreted with considerable caution.

The development of the organisms concerned in the decomposition of cellulose can be followed by the hanging drop method. Drops of mineral solutions containing some cellulose fibers as the sole source of energy were placed on cover slips and inverted over cavities in slides and sealed with vaseline. Two different mineral solutions were used, one adjusted to pH 5.2, the other one to pH 7.5. The drops were inoculated with cultures of bacteria or with neutral soils.

In the acid medium, the fungi begin to appear within 36 to 48 hours and rapidly overgrow the whole field.

In the neutral medium, the fungus mycelium is apparent only after 3 or 4 days; at that time also, a few bacteria can be seen around the cellulose fibers. A few days later, the bacteria reach enormous numbers but are very locally distributed, at the free ends of the fibers and at a few spots along the fibers. It was thought at first that the colonies were developing outside the fibers. However, Gray and Chalmers ('24) have reported that their culture of *Microspira agar liquefaciens* enters the cellulose fibers and multiplies in the central canal. It is therefore possible that, in the present case, the bacteria develop within the fibre and then break through, forming masses at certain points.

After a few more days the bacteria cover large parts of the field. The fungi develop also, but less than in the acid medium, this being due probably to the exhaustion of available nitrogen.

2. *Studies in Sterile Soils*.—Sterilization by heat alters greatly the physical and physico-chemical properties of the soil and thereby upsets the results of biological studies. On the other hand, the fact that an organism can carry on the decomposition of a certain nutrient in sterile soil is no proof that, under natural conditions, it will play a part in this process, because under these conditions there is the competition of other organisms. Finally, we must reckon with the difficulty of obtaining a uniform inoculation throughout the soil, as will be discussed later.

With all of these limitations in mind, the following experiments have been carried out.

Influence of Reaction (pH) on the Growth of Cellulose Bacteria.—A number of samples of the same soil (pH 5.2) were adjusted to a series of reactions ranging from pH 3.5 to pH 8.5., by addition of H_2SO_4 and $CaCO_3$. When the reaction of the soil had reached an equilibrium following the addition of acid or base, 0.5 per cent cellulose was added, and the soils thus adjusted were inoculated with a suspension of fresh neutral soil. After incubation for one month, the "numbers" of cellulose decomposing bacteria were determined by the dilution method; the results are presented in Table I.

TABLE I. *Effect of reaction of the soil on the numbers of cellulose decomposing bacteria*

Reaction of the soil (pH)	Numbers of cellulose decomposing bacteria
8.7	0
8.5	250,000
8.2	25,000,000
7.5	25,000,000
7.0	25,000,000
6.5	25,000,000
6.0	250,000
5.2	0
4.5	0
4.0	0

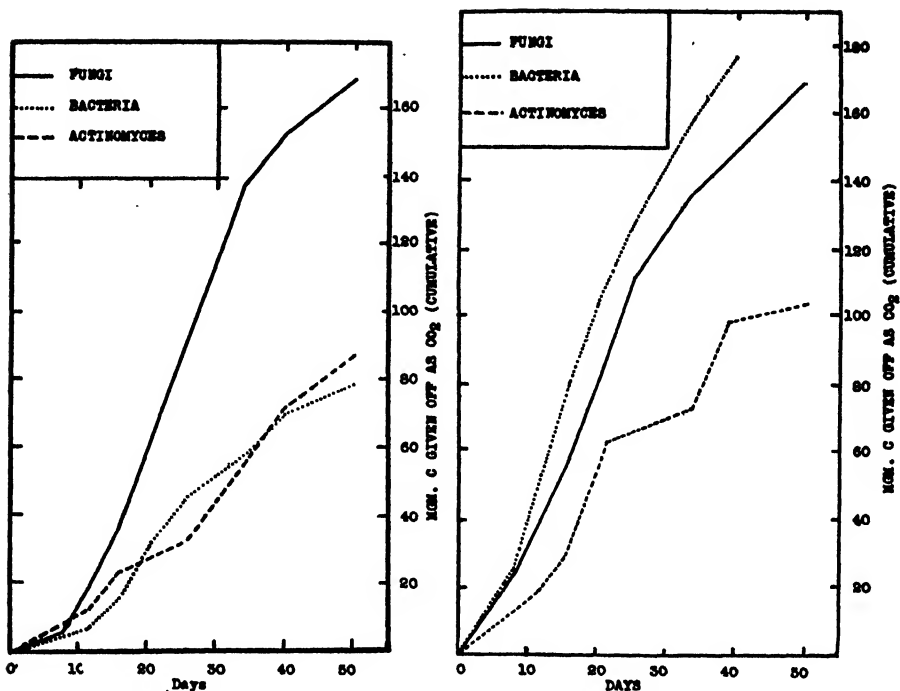
In the original soil (pH 5.2) it has never been possible to observe any development of cellulose decomposing bacteria subsequent to the addition of cellulose. This experiment demonstrates that the only factor involved in this phenomenon is the reaction of the medium.

Influence of Moisture

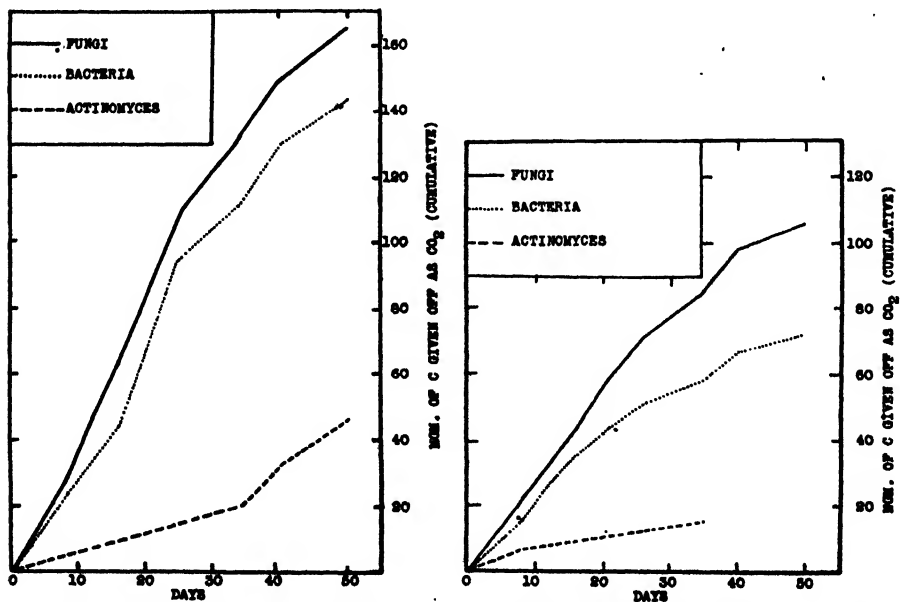
It becomes apparent that, at neutral reaction, certain fungi, actinomyces and aerobic bacteria are capable of decomposing cellulose. An attempt was made to determine the comparative rate of their action under different conditions of moisture.

Samples of 200 gm. of a neutral soil were placed in flasks with 750 mgm. of cellulose and 25 mgm. of $(NH_4)_2SO_4$. The samples were adjusted to different moisture contents (respectively 30, 50, 80, 95 per cent of the moisture holding capacity, and excess of water) and sterilized. A series of flasks was inoculated with: (a) a mixture of cellulose decomposing fungi, (b) an impure culture of *Spirochaeta cytophaga* (the impurity being a short rod unable to decompose the cellulose), (c) a mixture of two cellulose decomposing actinomyces.

The flasks were incubated at 28° C. and the CO_2 evolution recorded periodically as an index of cellulose decomposition. (Table II and figures 1, 2, 3, 4.)



FIGS. 1 AND 2. Comparative growth of cellulose decomposing bacteria, fungi and actinomycetes in a neutral soil. FIG. 1 (left) at 30 per cent moisture holding capacity; FIG. 2 (right), at 50 per cent moisture holding capacity.



FIGS. 3 AND 4. Comparative growth of cellulose decomposing bacteria, fungi and actinomycetes in a neutral soil. FIG. 3 (left) at 80 per cent moisture holding capacity; FIG. 4 (right), at 95 per cent moisture holding capacity.

TABLE II. *Influence of soil moisture on the decomposition of cellulose by different groups of microorganisms*

Organism	Soil moisture, % moist. holding capac.	Mgr. of carbon given off as CO ₂ between the following periods of incubation (in days)							
		0-8	9-12	13-16	17-21	22-26	27-34	35-40	41-50
Mixture of cellulose decom- posing fungi.....	30	5.5	14.0	15.5	30.0	32.5	39.0	16.5	15.5
	50	22.5	16.0	17.5	26.5	29.5	24.0	14.0	18.5
	80	29.5	17.5	17.0	24.5	23.0	20.5	16.5	16.5
	95	22.0	11.5	10.0	15.0	12.5	12.5	13.5	8.5
	Excess	—	—	4.5	—	—	3.0	—	—
Impure culture of <i>Sp. cyto- phaga</i>	30	—	7.0	8.5	16.5	14.0	12.0	12.0	8.5
	50	23.5	28.0	28.5	23.0	23.0	31.0	20.5	—
	80	23.0	9.5	11.0	28.0	21.5	18.0	18.0	14.5
	95	15.5	11.5	8.5	8.5	7.0	7.0	8.5	5.5
	Excess	—	1.0	—	—	—	1.5	—	—
Mixture of cellulose decom- posing actinomyces.....	30	—	12.0	10.5	—	15.0	17.5	16.5	15.0
	50	12.5	6.0	10.5	33.5	—	15.0	15.0	11.0
	80	5.0	—	—	—	—	15.0	11.0	15.0
	95	7.0	—	—	—	—	8.0	—	—
	Excess	—	—	—	—	—	3.0	—	—

TABLE II.—Continued

Organism	Soil moisture, % moist. holding capac.	Total C given off as CO ₂ in mgm.	Cellulose decomposed
Mixture of Cellulose decomposing fungi.....	30	168.5	525 mgm.
	50	168.5	528 "
	80	165.0	534 "
	95	105.5	345 "
	Excess	—	0 "
Impure culture of <i>Sp. cytophaga</i>	30	78.5	248 "
	50	177.5	590 "
	80	143.5	458 "
	95	72.0	233 "
	Excess	—	0 "
Mixture of cellulose decomposing actinomyces...	30	86.5	285 "
	50	103.5	330 "
	80	46.0	165 "
	95	—	0 "
	Excess	—	0 "

The results of this experiment seem to indicate that a low moisture retards somewhat the growth of the fungi at the beginning (probably retardation in

the germination of the spores). Their ultimate action seems to be equally good between 30 and 80 to 90 per cent of the moisture holding capacity.

On the contrary, optimum moisture for *Spirochaeta cytophaga* is very narrow. This organism requires a moist but well aerated medium, which fact is confirmed by the observation that, in liquid medium, it grows only at and slightly above the surface. We believe that the most active aerobic cellulose bacteria would behave the same way.

The actinomycetes also have their maximum at 50 per cent moisture, although they grow well in drier soils. Their activity decreases rapidly at a higher moisture.

What happens in a natural soil, where the factor of competition is introduced, is very hard to predict. Perhaps some insight can be obtained in this problem by the second part of the experiment.

Another series of the same soils was inoculated with a suspension of a neutral soil, to which had also been added a mixture of all the inocula-used previously. After incubating for 27 days, the numbers of fungi, actinomycetes and cellulose decomposing bacteria were determined (Table III).

TABLE III. *Influence of the moisture content on the abundance of different cellulose decomposing organisms in soil*

Per cent of moisture holding capacity	Bacteria	Actinomycetes	Fungi
30	20,000	14,000,000	1,500,000
50	20,000,000	600,000	1,300,000
80	20,000,000		1,400,000
95	2,000,000	400,000	1,900,000

The case of the actinomycetes in particular is a striking example of the importance of competition between different forms in the soil system. Although they have their optimum at 50 per cent moisture in sterile soil, the activity of the bacteria and fungi prevent their action at this moisture in normal soils. On the contrary, their numbers increase enormously in very dry soils where the bacteria and fungi are less active.

Comparative Growth of Cellulose Decomposing Bacteria and Fungi in a Fertile Neutral Soil

Spirochaeta cytophaga was unfortunately the only cellulose decomposing bacterium available for study when the preceding experiment was carried out. In order to get a better idea of the relative activities of bacteria and fungi in the process of cellulose decomposition, the following experiment was carried out.

To 100 gm. of a fertile neutral soil were added 100 mgm. of NaNO_3 , 100 mgm. K_2HPO_4 , 1 gm. CaCO_3 , enough moisture to bring to 60 per cent

of the moisture holding capacity and 500 mgm. of filter paper. After sterilization, duplicate samples were inoculated with (a) a mixture of cellulose decomposing fungi isolated from the soil (a *Trichoderma*, a green *Penicillium*, and a black unidentified mold), (b) a mixture of cellulose decomposing bacteria isolated from the soil (Spirochete, yellow vibrio, colorless vibrio, (c) a soil suspension. The evolution of CO₂ was recorded periodically (Table IV).

TABLE IV. *Comparative growth of bacteria and fungi in a fertile neutral soil*

Inoculum	Mgm. of C given off as CO ₂ during the following incubation periods (in days)						Total
	0-5	7-9	10-15	16-22	23-29	30-36	
Fungi.....	15.0	9.1	15.1	15.4	11.3	12.3	78.2
Bacteria.....	11.9	5.1	14.0	14.6	11.7	11.3	68.6
Soil suspension.....	13.6	7.7	16.7	16.8	15.7	14.9	85.4

The numbers of organisms were not determined in this experiment. Bacteria and fungi seem to be about equally active in the recomposition of cellulose in neutral soils. It was expected that the decomposition would be much more rapid in the presence of both groups, but this does not appear to be the case.

It is possible that the lack of a proper inoculation prevents the cellulose decomposing bacteria from being as active as they would be in a normal soil. While the fungi can rapidly spread throughout the whole mass of soil by the growth of their mycelium, it is perhaps hard for the bacteria to pass from one fragment of paper to another. In a normal soil, each fragment of cellulose is in contact with a number of cellulose bacteria, which have therefore a better chance to overgrow the fungi.

Studies in Normal Soils. The Decomposition of Cellulose in Two Fertile Soils of Acid and Neutral Reactions

The preceding data indicate that the activity of cellulose decomposing bacteria is greatly affected by the soil conditions. Some of the factors influencing their development may be suggested by the following study in which two different soils were used which were known to have about the same power of cellulose decomposition, but very different floras. These two soils are 5A (pH 5.5) and 5B (pH 6.8) of the soil fertility plots of the New Jersey Experiment Station. These soils were compared with and without cellulose, with and without combined nitrogen. To 100 gram portions of soil there was added 500 mgm. of cellulose and 100 mgm. of (NH₄)₂SO₄. The samples of the neutral soil received also 1 gm. of CaCO₃ and 50 mgm. of K₂HPO₄. The samples of acid soil received 50 mgm. of KH₂PO₄. The CO₂ evolution is recorded in Table V.

TABLE V. *Cellulose decomposition in two fertile soils of acid and neutral reactions*

Soil Samples	pH	Mgm. of C given off as CO ₂ within the following incubation periods (in days)					Cellulose decom- posed per cent	Nos. of cellulose bacteria	Nos. of cellulose- decomposing fungi
		0-9	10-18	19-27	28-36	Total			
1A Control	5.4	—	—	—	—	—	—	0	87,000
2A + cellulose	5.4	8.1	20.8	15.0	19.7	63.6	55	50,000	353,000
3A + cellulose + nitrogen	5.4	20.9	57.5	14.9	29.5	122.8	96	10,000	2,700,000
4B Control	6.8	—	—	—	—	—	—	1,000	43,000
5B + cellulose	6.8	9.9	20.3	13.3	16.9	60.4	53	5,000,000	110,000
6B + cellulose + nitrogen	6.8	28.4	58.6	13.7	30.5	130.2	99	10,000,000	490,000

It is interesting to note that, while soils 2 and 5 on one side, 3 and 6 on the other, exhibited the same ability to decompose cellulose, as shown by the rate of CO₂ evolution and the amount of cellulose decomposed, the numbers of fungi are much larger in the acid soils. This fact, added to the presence of large numbers of cellulose bacteria in the neutral soils, points emphatically to the important role of bacteria in the decomposition of cellulose in such soils.

It is important to notice here that the addition of nitrogen salts has no appreciable influence on the types of organisms developing as a result of the addition of cellulose. This is not surprising when it is considered that all cellulose decomposing bacteria, as well as fungi, require large amounts of combined nitrogen to carry on their activities.

That fungi are very active in the process of cellulose decomposition, even when no nitrogen is added to the soil, is further demonstrated by another experiment not described here. Soils kept at 33, 66, and 100 per cent saturation received 1 per cent cellulose with or without nitrogen. In all cases the soils receiving nitrogen decomposed cellulose much more rapidly, but in all the aerobic soils (33 and 66 per cent saturation), the numbers of fungi increased enormously, irrespective of the addition of combined nitrogen. The soils used in this experiment were acid (pH 5.8).

The Nature of the Organisms Responsible for the Decomposition of the Cellulose of Straw

Cellulose is not applied to the soil as pure cellulose, but in the form of complex materials, especially as straw. In the following experiment, the nature and numbers of organisms developing as a result of the addition of straw and filter paper have been compared.

Samples of 200 gm. of soils 5A and 17A, 5B and 17B of the soil fertility plots of the New Jersey Experiment Stations, were brought to 60 per cent of their moisture holding capacity. Cellulose was applied either as filter paper or corn straw in the proportion of 0.5 per cent of the weight of the

soil. Enough $(\text{NH}_4)_2\text{SO}_4$ and K_2HPO_4 was also added. The samples were incubated at room temperature.

Determinations of the numbers of cellulose decomposing bacteria were made after 15 and 30 days, the results being as follows (Table VI).

TABLE VI. *Numbers of cellulose decomposing bacteria developing as a result of the addition of filter paper or straw to the soil*

Soil samples	pH	Numbers of cellulose bacteria per gram of soil	
		After 15 days	After 30 days
5A + straw.....	5.5	0	0
17A + straw.....	5.4	0	0
5B + straw.....	6.8	10,000,000	5,000,000
17B + straw.....	6.8	2,000,000	5,000,000
5B + paper.....	6.8	20,000,000	50,000,000

We see that the cellulose decomposing bacteria are unable to act in acid soils whether straw or pure cellulose is applied. It is also interesting to note that the organisms developing in the samples having received straw are the same as the organisms obtained in the case of filter paper; *Spirochaeta cytophaga* in particular was obtained in both cases.

Groups of Organisms Decomposing Cellulose under Soil Conditions Favorable for Fungi, Actinomyces and Bacteria

A study of the rate of carbon dioxide evolution does not indicate which groups of organisms are chiefly responsible for the decomposition of cellulose when conditions in the soil are favorable for the development of fungi, actinomyces and bacteria. It was hoped that by determining which group of organisms started to develop first, some information could be obtained on the subject.

Two soils were used which had been subjected to the same set of treatments for a number of years, except that one of them had and one had not received addition of lime. These soils are 17A (pH 5.3) and 17B (pH 6.8) of the soil fertility plots of the New Jersey Experiment Station. One kilogram samples were used. The moisture content was brought to 60 per cent of the moisture holding capacity. Some of the soils received 0.5 per cent filter paper, others 0.5 per cent straw, and all 750 mgm. of $(\text{NH}_4)_2\text{SO}_4$. The neutral soils received in addition 2 gm. of CaCO_3 .

The numbers of organisms were determined daily for the first five days, then at longer intervals of time; for the bacteria the dilution method was used and, for the fungi, the acid medium. In order to get representative samples, five gram portions of soils were used. These were thoroughly shaken in 100 cc. water blanks, 2 cc. portions of this suspension being used for further dilutions. The results are presented in Table VII.

TABLE VII. *Influence of cellulosic materials on development of soil microorganisms under both acid and neutral conditions*

Numbers of organisms are expressed as thousands per gram of soil

Incubation in days	17A—Control pH 5.2			17A—paper pH 5.2			17A—straw pH 5.2		
	Fungi	Bact.	Act.	Fungi	Bact.	Act.	Fungi	Bact.	Act.
0	48	0							
1	69	0		39	0		64	0	
2	120	0		133	0		490	0	
3				140	0		545	0	
4	110	0		800	0		2,100	0	
6				1,100	0		?	0	
7				1,870	0		2,700	0	
8				1,400	0		2,500	0	
10				2,700	0		2,400	0	
13	58	0	290	3,950	0	228	2,450	0	180
17				3,800	0		1,980	0	
21				4,060	0		3,050	0	
28				5,050	0		2,100	500	
35				4,480	0		2,200	0	

TABLE VII.—Continued

Incubation in days	17B—Control pH 6.9			17B—filter paper pH 6.9			17B—straw pH 6.9		
	Fungi	Bact.	Act.	Fungi	Bact.	Act.	Fungi	Bact.	Act.
0	23	2							
1	36	20		40	2		38	2	
2	33	10		60	10		80	10	
3				75	10		75	100	
4	40	2		63	50		65	100	
6			1,890	160	1,000	1,460	160	10,000	2,030
7				100	10,000		370	10,000	
8				160	10,000		250	50,000	
10				370	100,000		520	10,000	
13	31	2	1,500	470	1,000,000	1,690	230	10,000	3,370
17				425	1,000,000		400	1,000	
21				530	100,000		600	10,000	
28				470	10,000		950	10,000	
35					10,000			10,000	

It is also interesting to note that, even in the acid soils which received straw, the numbers of bacteria which developed on the starch agar plates were very small.

It seems evident therefore that the greater activity of fungi in acid soils is not limited alone to the decomposition of cellulose.

The numbers of actinomycetes do not show any significant variation from the control except in the case of soil 17B which received straw. The increase observed in this case may be due to the influence of the numerous constituents other than cellulose which are present in straw. The results of Conn

('16) and Martin ('23) can be explained on the same ground; it would seem that, as far as the decomposition of true cellulose in normal soils is concerned, actinomyces play only a very limited role if any.

A study of the numbers of fungi shows correlations similar to those which have been observed before. The very rapid increase observed on the fifth day is probably more indicative of spore formation than of a proportional increase of the mycelium. In the acid soils, the numbers of fungi increase more rapidly with the straw than with the filter paper. This suggests that, at this time, the fungi have attacked the more soluble constituents of the straw in the acid soils.

The results concerning the numbers of cellulose decomposing bacteria confirm all previous statements.

Comparative Studies of the Nature of the Cellulose Decomposing Flora Present in the Soils from Humid and Arid Regions

All of the work reported above has been carried on with soils of humid regions or with organisms isolated from such soils. On the other hand, most of the organisms described by Kellerman, McBeth and associates were obtained from soils of arid or semi arid regions. Since the results obtained from these two regions appear to be so different, it was of interest to compare typical soils from humid and arid regions.

Five different soils were used, two from the soil fertility plots of the New Jersey Experiment Station and three from California. They were all brought to a moisture corresponding to 50 per cent of the moisture holding capacity and all received 0.5 per cent cellulose (as filter paper) with a proper amount of $(\text{NH}_4)_2\text{HPO}_4$. The samples were incubated at 28° C. and the numbers of organisms determined after 5, 10 and 30 days (Table VIII).

TABLE VIII. *Comparative growth of cellulose decomposing bacteria and fungi in three Californian and two New Jersey soils*

Days of incubation	Soil Sample	1C—Davis California	30—Fresno California	Berkeley California	5B—New Jersey	17A—New Jersey
	PH	7.0	7.5	7.0	6.8	5.2
5	Fungi . . .	75,000	78,000	50,000	94,000	700,000
	Bacteria..	500,000	50,000,000	500,000	50,000,000	0
10	Fungi . . .	260,000	60,000	210,000	780,000	1,320,000
	Bacteria..	10,000,000	100,000,000	500,000	500,000,000	0
30	Fungi . . .	165,000	53,000	110,000	266,000	2,900,000
	Bacteria..	10,000,000	5,000,000	500,000	100,000,000	0

These results show that the neutral or alkaline soils of the dry regions behave very much like the neutral soils of humid regions. Furthermore, the organisms developing at the highest dilutions are very similar in both cases.

The two organisms which predominated in the Californian soils were *Spirochaeta cytophaga* and a very long thin rod which failed to grow on meat peptone agar but produced large colonies on starch agar. More interesting is the fact that when such soils to which cellulose has not been added are inoculated into a mineral medium containing cellulose, a different transformation develops after 8 to 10 days than occurs after the soil has received recent applications of cellulose. The organisms responsible for this transformation have not been isolated yet. Their growth is less strictly aerobic than that of such organisms which develop abundantly on cellulose in soils. Growth appears as a decomposition of the paper below the surface of the medium and the organisms require a much longer time to manifest their action. In many respects they appear similar to the organisms obtained by Kellerman and McBeth.

Decomposition of Cellulose in Soil under Anaerobic Conditions

A strict anaerobe, capable of decomposing cellulose very rapidly, was obtained from a cranberry bog of New Jersey. One per cent cellulose was added to such a soil; after 2 months incubation under water, dilutions of this soil were inoculated into test-tubes containing 15 cc. of a peptone medium with a fragment of filter paper. The test tubes were incubated at 28 to 30° C. in an atmosphere of hydrogen. Decomposition of the paper took place up to 1 : 100,000 dilution.

Two samples of the same soil kept respectively at 70 and 50 per cent of the moisture holding capacity gave growth up to a dilution of 1 to 10,000; no growth was obtained from soils kept at 30 per cent of the moisture holding capacity. A thorough shaking of the soil is essential to obtain growth at high dilutions due to the fact that the cellulose fermenters cling to the fibres and are present in the suspension in very small numbers.

In another experiment, the rate of the decomposition of cellulose was followed in samples of the same soil brought to 33, 66 or 100 (with excess of water) per cent of the moisture holding capacity, containing one per cent of cellulose with or without the addition of nitrogen. The details of the results will not be reported here. But it may be said that in all the samples kept under aerobic conditions (33 and 66 per cent of the moisture holding capacity) decomposition set in after 2 days incubation; on the contrary, it took 14 days for the decomposition to set in under water. This points to the difference of flora active under the different conditions.

In order to see whether it is the lack of the proper flora or other factors which are the cause of the long period of time required for anaerobic decomposition of cellulose to set in, the following experiment was carried out.

One hundred gram portions of soil containing 1 gm. of cellulose and 20 mgm. of $(\text{NH}_4)_2\text{HPO}_4$ were sterilized and very heavily inoculated with a suspension of a very active anaerobic cellulose decomposing organism (impure

culture obtained from anaerobic soil). The cultures were incubated in a vacuum of about 15 mm. mercury. The CO_2 evolution was determined periodically by evacuation of the gases (Table IX).

TABLE IX. *Rate of cellulose decomposition in a soil kept under water and heavily inoculated with anaerobic cellulose decomposers*

Incubation (in days)	C evolved as CO_2 (in mgm.)
0-8	5.5
9-12	5.2
13-16	6.8
17-21	21.1
22-26	22.2
27-34	30.3
35-40	22.1
41-50	22.7

It is apparent that, in spite of the presence of large numbers of the proper organism, 16 days elapsed before decomposition became active.

These results are apparently contradicted by the fact that, when new quantities of cellulose are added to an anaerobic soil in which cellulose decomposition has been recently very active, the decomposition sets in immediately. No doubt, the abundance of the proper organisms is an important factor, but perhaps more important is the fact that, after a soil has been kept under anaerobic conditions for a certain time, it has become a favorable medium for anaerobiosis. Quastel and Stephenson ('26) have demonstrated that the advantage of using a large inoculum in transfers of *B. sporogenes* is not in the large numbers of organisms introduced, but in the addition of certain compounds which give to the medium a proper reduction potential. Working with a proteolytic organism. Quastel found that glutathione or cysteine or similar compounds (containing an SH-group) played the same role as a large inoculum. It is possible of course that the products of anaerobic decomposition of the cellulose result in the same effect.

DISCUSSION

It will be realized that only very few factors have been investigated as to their influence on cellulose decomposition; studies of the importance of certain radicals, and of soil organic matter have not been developed because they did not promise any accurate information.

On the other hand, the differentiation between fungi, actinomycetes and bacteria as physiological groups seems very crude. Nevertheless, the facts reported in these pages seem to warrant the following generalizations.

Under acid conditions fungi are the only organisms that appear to decompose cellulose. In acid soils the course of the decomposition is about the same whether we are dealing with sterilized soils inoculated with cultures of

fungi or with the normal soils. Furthermore, the "numbers of fungi" increase enormously in the acid soils which have received cellulose. We conclude therefore that fungi are the dominating, if not the exclusive agents of the decomposition of cellulose in acid soils.

In neutral or slightly alkaline soils there is a large development of bacteria. Here the moisture factor seems to be very important. The actinomyces have an optimum at 50 per cent saturation but, even under these conditions, their growth is slow and they are overgrown by the fungi and bacteria. In normal soils, the competition limits their activities to conditions where the soils are fairly dry.

Aerobic bacteria seem to thrive best at 50 to 80 per cent of the moisture holding capacity. It is possible that some groups of bacteria which have not been studied extensively enough are also very active at higher moistures. The fungi are also at an optimum between 50 and 90 per cent moisture, but on the whole it seems reasonable to believe that in normal, moist but well aerated soils, bacteria and fungi are equally active.

About two weeks elapsed before the anaerobic cellulose decomposing flora became established in a soil kept under water.

It may be argued that the results obtained by Waksman and Skinner ('26), concerning the activity of fungi in the process of cellulose decomposition, hold only when large amounts of combined nitrogen are applied. Against this suggestion, there are the two following facts:

(a) Cellulose decomposing bacteria have about as high nitrogen requirements as the fungi.

(b) Although it is possible that the products of cellulose decomposition by bacteria may serve as sources of energy for nitrogen fixation, unpublished results seem to indicate that very little nitrogen is fixed in such a manner in the soil. Furthermore, other experiments show that, even if such a nitrogen fixation actually takes place, the accumulation is so slow that it does not affect appreciably the decomposition of the cellulose.

SUMMARY

The influence of certain environmental factors on cellulose decomposition was studied by the following methods: (a) direct microscopic examination; (b) determination of the numbers of cellulose decomposing bacteria, actinomyces and fungi; (c) rate of CO_2 evolution; (d) amount of cellulose decomposed, when cellulose is added to normal or to sterile soils inoculated with pure and mixed cultures.

The following conclusions have been reached:

(a) The presence or the absence of an abundant supply of combined nitrogen does not have any appreciable influence on the nature of the organisms concerned in the decomposition of cellulose in the soil.

(b) In acid soils under aerobic conditions, fungi are the only agent active in the decomposition of cellulose.

(c) In neutral, very slightly acid or slightly alkaline soils, the moisture factor is one of the most important in determining the nature of the organisms which develop.

(d) The activities of the actinomycetes are limited to the dry soils, as their slow growth does not enable them to compete with bacteria or fungi in humid soils.

(e) In neutral, very slightly acid and slightly alkaline soils at an optimum moisture (60 to 80 per cent saturation), bacteria are probably as active as or perhaps more active than the fungi.

(f) In normal soils kept under water, a lag period of 14 to 16 days is observed before an active decomposition of the cellulose sets in; this is due not only to the absence of an active anaerobic flora but perhaps more to the lack of a proper medium for anaerobiosis.

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MYCORRHIZA OF SOUTHERN PINES

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INTRODUCTION

While lifting pine seedlings in a nursery of the Southern Forest Experiment Station at Bogalusa, Louisiana, in December, 1926, the writer noticed that the roots possessed numerous mycorrhiza. This led to a further study of the mycorrhiza in the field and laboratory.

The writer is indebted to the members of the Station staff for furnishing material from different Southern states, and to Professor W. T. Penfound for offering the facilities of the botanical laboratory of Tulane University, where most of the histological work was carried on.

HISTORICAL

Much work on mycorrhiza has been done since the appearance of the classic paper by Frank in 1885. Some 70 or 80 papers have been published since then, but the actual effect of the mycorrhiza on the host plant is still in dispute. Some of the earlier writers and also some very recent ones regard the mycorrhizal association chiefly as a parasitic relationship, though not always very harmful to the host. Others, on the contrary, consider such a relationship of the fungus with the root of the host a symbiotic one, and therefore highly beneficial to the host plant.

It is needless to review the earlier papers in detail, for many of them present rather inadequate data and presumably erroneous observation. But, as the writer regards the question of the importance of mycorrhiza to forest trees a vital one, especially for the forester, he feels justified in summarizing briefly the diverse views held by recent writers as to the actual relation of mycorrhiza to trees.

Nearly three decades ago Stahl ('00) found mycorrhizas confined largely to soils poor in nitrogen and mineral salts. This observation led him to suggest that the fungus is beneficial to the "host" plant mainly in its ability to supply salts to the roots which it inhabits.

McDougall ('14) in his study of the mycorrhizas of *Carya*, *Quercus*, *Betula*, and other forest trees found by his glass plate method the rate of growth of infected roots to be rather rapid; a day or two is needed to complete the mantle formation. It is the formation of the mantle that retards the root growth. He found that numerous fungi produce mycorrhiza. In fact, any of the common mushrooms are capable of producing mycorrhiza.

Apparently, a seasonal relation exists in the development of mycorrhiza, for they are abundant in the autumn and practically absent in the spring. This seasonal occurrence leads him to regard mycorrhiza as annuals, beginning their development during the summer and completing their life cycle in the autumn. McDougall regards the mycorrhizal relationship chiefly as a parasitic one. This theory is again brought out in his later paper on mycorrhizas of conifers (McDougall '22) and also in his recent paper (McDougall and Jacobs '27).

Several years later Melin ('22) found that on *Pinus sylvestris* the mycorrhiza were distinctly ectotrophic and branched while on *Picea Abies* they were monopodial. He classified the fungi which produce mycorrhiza according to the appearance of their mycelia and named them *Mycelium Radicis silvestris* on *Pinus* and *M. R. Abietis* on *Picea*. He found that in pure cultures the fungus grows very slowly, but when in contact with a tree seedling, the rate of growth is markedly increased. Roots of pine are more readily infected in sand than in human cultures. Infection takes place through the root hairs or epidermal cells. Without mycorrhizal infection, seedlings of pines develop root hairs, but not where mycorrhiza are present. Melin ('23) again shows in a later paper that the fungi which produce mycorrhiza on roots of coniferous trees are various species of *Boletus*, *Amanita*, and *Tricholoma*. He further asserts that the root of the tree and the fungus live in a mutual symbiosis. This he concludes from cultural observation, from field observation, and from anatomical studies. Melin ('24) also found that mycorrhizal growth is poorest on pH 3.5 and best on pH 5.0. In a paper published the same year, he attempts to show that mycorrhiza aid in nitrogen-fixation, a statement made by earlier writers but vigorously disputed because of the apparent impossibility of sterilizing the mycorrhiza so as to remove nitrogen fixing bacteria, which cling to the roots of the plants. In two other papers Melin ('24 and '25), after a thorough study of the importance of tree mycorrhiza, states that such a relationship between fungus and root of trees is of great benefit to the tree and of importance in development of forests, for the fungus apparently replaces the root hairs in the function of transference of water and salt to the roots. This does not mean, however, that it may do so more efficiently than the root hairs.

Masui ('26) in a recent paper discusses the renewal of growth of the mycorrhiza, and states that "when the root is weak it can not grow more after completion of the mantle. If, however, the root still possesses the capacity for further growth, there arises a struggle between the root and the mantle. But after a pause some vigorous roots are impelled to new growth, split the mantle and peep out—the renewed growth through the living mantle. When the cortex of the root dies, the mantle also perishes." In another paper of the same year, Masui ('26) presents the results of a study of the mycorrhiza of *Abies firma* S. et Z., which he finds to be caused by *Cantharellus*

floccosus Schu. His microchemical investigations seem to indicate that the fungus causes a reduction of the starch in the cells of the pericycle. Similarly, ammonium salts and nitrates are also reduced in infected tissues. These results, if considered independently of the activities of the fungus in breaking down and rendering available the complex organic materials, would give the impression that the relationship is pure parasitism.

FIELD OBSERVATION

Observations at Bogalusa indicate that side roots of seedlings of *Pinus echinata* Mill., *P. palustris* Mill., *P. taeda* L., and *P. caribaea* Morelet are infected by fungi which cause a curtailment in growth resulting in the club-like appearance of the infected root tips. The infected roots fork repeatedly and dichotomously. In some cases the forked club-like root tips present the appearance of a coral-like mass. Each mature infected root when examined under a hand lens reveals a felted or hairy mantle capping the root. Such mantles surrounding the roots possess distinct colors, which make the mycorrhiza quite distinguishable even to the naked eye.

Mycorrhiza were present not only on the roots of seedlings examined at Bogalusa, but also in abundance on roots of *P. palustris* seedlings growing near McNeill, Mississippi. In most cases the mycorrhiza seem to be confined to the lateral roots close to the surface of the ground, and only in a very few cases have they been seen by the writer on lateral and tap roots deep in the soil. This confinement to the upper layers of the soil suggests the fungi to be aerobic organisms capable of association with the roots only in the presence of abundance of oxygen. It is due also to the greater amount of organic material and acid reaction near the surface.

The observations thus far made in the field do not justify the writer in expressing any definite opinion as to the type of soil best suited for mycorrhizal association. Seedlings of pine bearing mycorrhiza were found in sandy loams of the Norfolk type and also in Orangeburg fine sandy loam. Specimens of mycorrhiza on *P. palustris* were also received from mature trees of the Florida National Forest. These were found on the roots of trees growing in almost pure sand, and resembled a coral-like mass.

LABORATORY STUDIES

Microscopic studies indicate that fungi producing mycorrhiza on the pines in the Southern states are of the Hymenomycetes group. However, no definite determination could at this time be given owing to the lack of fruiting bodies on the material at hand. The mycelium which forms the mantle has the appearance of a pseudo-parenchymatous tissue, because of its interwoven and interlaced structure.

The mycorrhiza of *P. echinata* measure about 1.5 mm. long and 0.5 mm. in diameter. They are dichotomously branched in most cases and are silvery

gray in color when young, turning to ash gray with age. Those of *P. taeda* are somewhat longer, being 2.0 mm. long and 0.5 mm. in diameter. They also are dichotomously branched but are yellowish when young and turn to grayish brown with age. The mycorrhiza of *P. caribaea* are somewhat similar to those of *P. taeda* but become silver gray when mature. *Pinus palustris* possesses mycorrhiza considerably longer than the preceding ones, averaging 2.5 mm. in length and 0.7 mm. in diameter, and ranging in color from buff when young to light brown when mature.

In cross-section the pseudo-parenchymatous structure of the mantle is quite distinct in all of the four species. The diagrams in Plate I show the general appearance of the mantle, the cortical cells and the central cylinder. Only in *P. echinata* has the writer been able to observe actual distortion of the epidermal cells by the hyphae of the mantle. In all other cases the mantle was resting against the epidermis of the root, and the cells of the latter appeared to be uninjured. All indications seem to show that the mycorrhiza of the pines of the Southern States are distinctly of the ectotrophic type, as no penetration of the fungus into the cells has been found.

DISCUSSION

It seems obvious from a review of the literature that practically no work has thus far been done on the mycorrhiza of American pines. Ashe ('15, p. 42) states: "The symbiotic mycorrhiza, which occurs on the roots of the pocoson pine (*P. serotina*) and enables it to grow in the wet and unaerated soils of pocosons, briery bays, fetter-bush bays, red swamps and peat bogs, does not occur on loblolly pine, which possibly explains the absence of this tree from such sites." McDougall ('22) reports mycorrhiza found by Barrington Moore on *Pinus strobus*, *Abies balsamea* Mill., and *Picea rubra* Link. The same writer has previously described ('14) mycorrhiza on hardwood trees in which he regards them as merely chance associations, the fungus being the parasite. Only in maple does he regard the endotrophic mycorrhiza as a case of pure symbiosis. In the pine, however, he looks upon the ectotrophic mycorrhiza as a sort of a sclerotium where food is stored by the fungus for fruit production. In other words, he regards the fungus of the mycorrhiza as a definite parasite on the roots of the pine. In a very recent paper (McDougall and Jacobs '27) mycorrhiza found on the roots of *Pseudotsuga mucronata*, *Pinus Murrayana*, *P. monophylla* and other conifers indigenous to the Central Rocky Mountain Region are described. The conclusion is reached that "the ectotrophic mycorrhiza . . . should be classed under antagonistic nutritive conjunctive symbiosis," in other words, ectotrophic mycorrhiza are considered by these authors a case of pure parasitism. This view is also held by Masui ('26) for *Abies firma*. But Melin in a series of papers ('22, '23, '24, and '25), seems convinced of the beneficial effects of the fungus on the tree. By a series of experiments he shows that mycor-

rhiza do not assimilate atmospheric nitrogen but are able to supply to the root ammonium salts as well as other inorganic salts, and that by means of mycorrhiza the host plant is able to convert more freely organic nitrogenous substances such as nucleic acids and peptones than through the roots themselves. Finally he regards mycorrhiza as symbionts of primary importance which function as organs of absorption of nutritive substances and aid in nitrogen assimilation. Should, however, the host plant be weakly developed, the fungus might get the upper hand, and become parasitic. Thus, Melin, after an intensive and detailed study of mycorrhiza of *Pinus sylvestris*, *Pinus montana*, and *Picea Abies*, regards mycorrhiza as being of vital importance to trees, and suggests their usefulness in practical forestry.

Waksman ('27) summarizing the conclusions thus far reached on the rôle of mycorrhiza in the nutrition of plants states that from the results obtained by various investigators it seems evident that the chief function of the mycorrhiza is to render available to the host plant the nitrogen which is present in the organic matter of the soil. In other words, the prime function of the fungus is not to bring into the plant nutrients, but to change the organic matter of the soil in such a way as to liberate the salts, and to make them available to the host plant. Melin, particularly is of the opinion that that is just what is happening when trees are growing in raw-humus; the fungus changes the humus, liberating the nutrients, and supplies them to the roots of the trees.

The writer's observations in the field and laboratory induce him to side with Melin's views. It seems inconceivable, at least to the writer, that seedlings which appear to be literally covered with mycorrhiza and yet seem perfectly vigorous should harbor a parasitic fungus. Judging by the abundance and degree of distribution of the mycorrhiza, and the vigorous and healthy condition of the seedlings, it seems more probable that the mycorrhiza may exercise a beneficial effect on the pines. Future work on mycorrhiza of American forest trees may possibly decide this question, at least as far as coniferous trees are concerned.

SUMMARY

1. Mycorrhiza were found in abundance on roots of seedlings of *Pinus palustris*, *P. echinata*, *P. caribaea*, and *P. taeda*.
2. The mycorrhiza occur mainly on the lateral branches of the roots in the upper layers of the soil.
3. The fungus producing the mycorrhiza is apparently of the Hymenomycetes group.
4. The abundance and the manner of distribution of the mycorrhiza together with the vigorous condition of the affected seedlings suggest that the fungus is a beneficial symbiont, not a parasite.

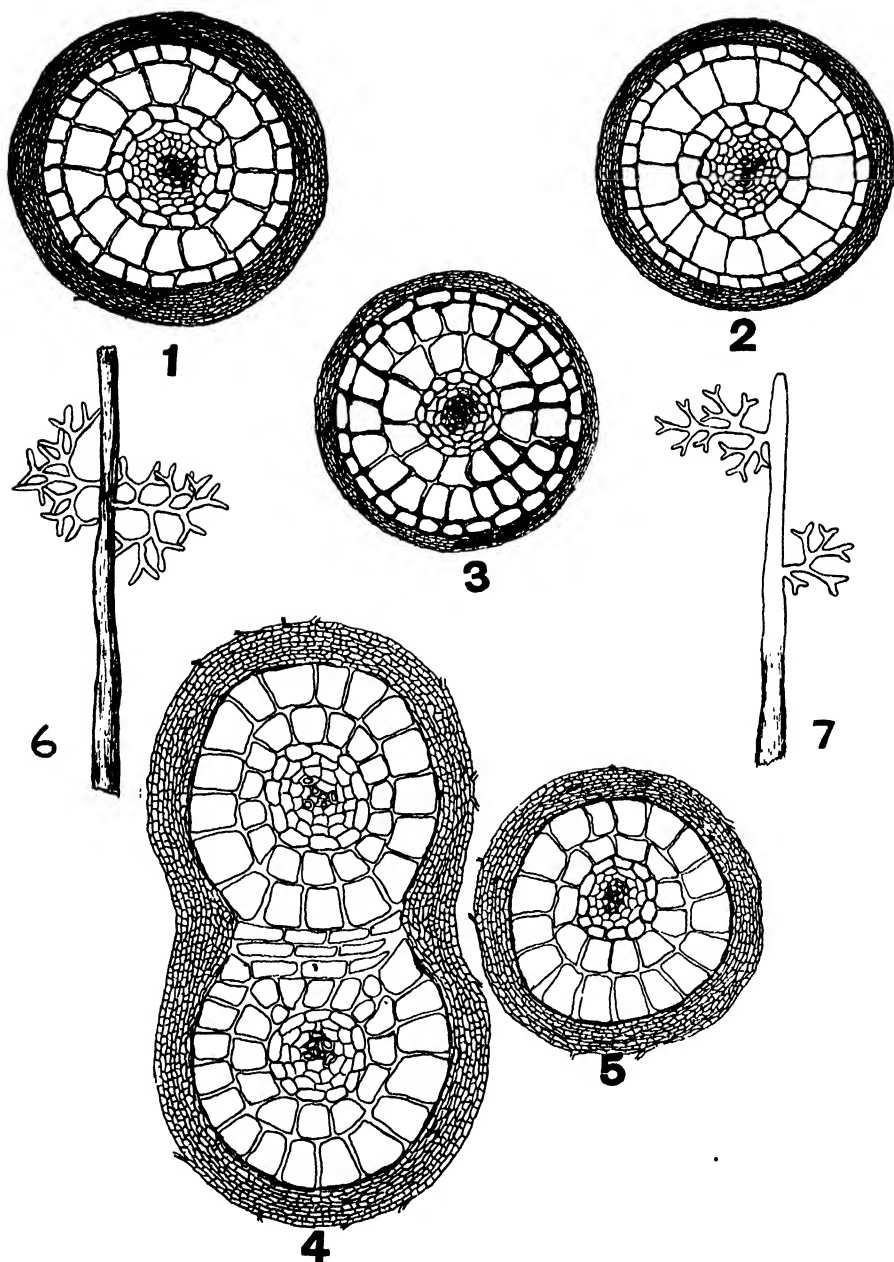


PLATE IV. 1. Cross-section of root of *Pinus palustris* showing the pseudo-parenchymatous appearance of the fungous mantle. 2. Cross-section of root of *Pinus taeda*. 3. Cross-section of root *Pinus echinata*. 4. and 5. Cross-sections of roots of *Pinus caribaea*. 6. Mycorrhizal cluster on a root of *Pinus caribaea*, showing the character of branching. 7. Mycorrhizal cluster on a root of *Pinus echinata*, showing the character of branching.

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HIBERNATION OF CERTAIN SCARABÆIDS AND THEIR TIPHIA PARASITES¹

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Our knowledge of the depth to which such insects as white grubs and May beetles penetrate the soil to escape the rigors of cold weather, and to pass their period of hibernation, is limited to a small number of casual observations. Only a few general statements pertaining to the subject are to be found in the literature. While writers assert that such and such a species passes the winter "below the frost line" or "below the plow line," no specific attention or careful study has been given to the subject. This is due, in part at least, to the difficulty of studying the habits of insects which live within the soil. Another factor involved, and perhaps the most important, is the difficulty of making specific identification of the immature stages of the specimens found in the soil. In most instances they must be reared through their developmental periods to the adult before they can be identified. Furthermore, winter studies of insects in the soil require careful excavation, involving considerable manual labor which must be done during the coldest and most disagreeable part of the year.

Criddle² records that in Canada the grubs of certain species of *Phyllophaga* and allied genera penetrate to a depth of 74 inches, and the beetles may burrow as deep as 47 inches during the winter. This statement indicates at what depth grubs may be found in a more northern climate, but no data are available in regard to the actual depth of the various species in the more temperate regions of the United States. No doubt the climate has a direct bearing on the subject, and the depth of penetration will vary with the region. In fact, the present study shows that white grubs do not penetrate as deeply in Kansas as Criddle observed in Canada. A discussion of the literature of this subject has been presented by McColloch and Hayes (1923).³

The depth at which these insects pass the winter is important in connection with the recommendation of fall, winter, or early spring plowing as methods of control. In order to recommend intelligently such practices, it is essential that definite information relative to the depth of hibernation of

¹ Contribution No. 356. Kansas Agricultural Experiment Station. This paper embodies some of the results obtained in the prosecution of the Stations project No. 100.

² Criddle, N. "The habits and control of white grubs in Manitoba." *Agr. Gazette of Canada*, 5: 449-454, 1918.

³ McColloch, J. W., and Hayes, Wm. P. "Soil temperature and its influence on white grub activities." *Ecology*, 4: 29-36. 1923.

such insects be available. It was primarily to secure data along this line that the studies herein reported were undertaken. It also seemed desirable to further check the studies of McColloch and Hayes (*loc. cit.* footnote 3) in the fall and spring reversals of temperature conditions on the surface and subsurface layers of soil, and the bearing of such changes upon the activities of soil insects in general.

METHOD

The present study was started during the winter of 1919-1920, and carried on at intervals, when time was available. All examinations were made by removing the soil with a spade to depths of 14 to 48 inches, depending upon the nature of the subsoil.

The size of the areas examined varied somewhat. In 1919-1920, eight holes were dug, each of which was three feet square. Four holes, each two by four feet, were dug during the winter of 1920-1921. No further digging was done until the fall and winter of 1922-1923, when 24 holes were sunk. These holes were usually four feet square, though a few were four by six in size. They varied in depth from 14 inches to 48 inches. In this connection it may be mentioned that in each case, digging was continued as long as insects were found. Only nine holes, two by four feet in area, were dug in the fall of 1923-1924. During the winter of 1925-1926, a series of 37 holes, two by four feet in area, were excavated.

In each operation, the soil was always removed inch by inch, broken up by hand, and carefully searched for insects. These were removed, given a number, and the immature stages taken to the laboratory cave for rearing and identification. Many of the grubs failed to mature, and in the case of the 1925-1926 collections, only a few had matured at the time this was written. The data for the 1922-1923 collection are the most complete, a greater percentage of the developmental stages of the various species having been reared to maturity.

During the 1919-1920 season, excavations were begun on October 24 and completed before severe weather arrived. The first hole in 1920-1921 was dug December 16, and the last on March 16. The 1922-1923 work began November 25 and was continued at frequent intervals until March 24. During the season of 1923-1924, the earliest hole was dug November 5 and the last, December 17. Hole No. 1 in 1925-1926 was dug November 20, and No. 37 on March 20. Obviously, the studies of the two seasons, 1922-1923 and 1925-1926, covering the entire winter, were the most complete. The March digging, however, showed so little difference from that of November that it is believed the early season work of 1919-1920 and 1923-1924 is as representative as that of the two years when work was prosecuted all winter.

PRESENTATION OF DATA

Hibernation of White Grubs in General

Since the various species of white grubs cannot be recognized, and furthermore, are difficult to rear, many dying before maturity, it was deemed advisable to record the depths at which all grubs, regardless of species, were found. These data are summarized for the five seasons in Table I which shows the number of specimens hibernating at different depths.

TABLE I. *Total number of white grubs hibernating at different depths*

Depth inches	Winter of					Total
	1919-20	1920-21	1922-23	1923-24	1925-26	
3			10	1	3	14
4	9		10	4	10	33
5	2	12	18		4	36
6			38	6	6	50
Plow line						
7	7		22	4	6	39
8	28		38	2	18	93
9	16	7	34	6	3	59
10	14		38	6	31	89
11	15	2	38	4	11	70
12	2	24	82	4	38	150
13	4	1	12	1	4	22
14	4	3	40	2	32	81
15	8	22	35	3	12	80
16	2	2	43	1	23	71
17		9	20		1	30
18	1	13	39	4	30	87
19	1	9	12	1		23
20		7	21		15	43
21	1	3	8		1	13
22	1	4	13		5	23
23		1	8	1		10
24		2	12	4	8	26
25	1	4	4		1	10
26		1	3	1	1	6
27		2	4			6
28		1	2	1		4
29						
30			3	3	2	8
31			1			1
32			2		1	3
33			1			1
34			1			1
35						
36			2		1	3
37			2			2
38						
39						
40			1			1
Total.....	116	129	617	59	267	1188
Per cent above 6 in.	9.5	9.3	12.3	18.6	8.6	11.2
Per cent below 6 in.	90.5	90.7	87.7	81.4	91.4	88.8

From Table I it will be observed that a total of 1,188 grubs were removed from the soil. Many of the grubs were reared to maturity, and the data concerning the various species identified will be discussed later. The data for the five seasons show that approximately 89 per cent were found below the depth of six inches, which will here be considered as the "plow line," or depth below which insects would be uninjured by winter plowing. The

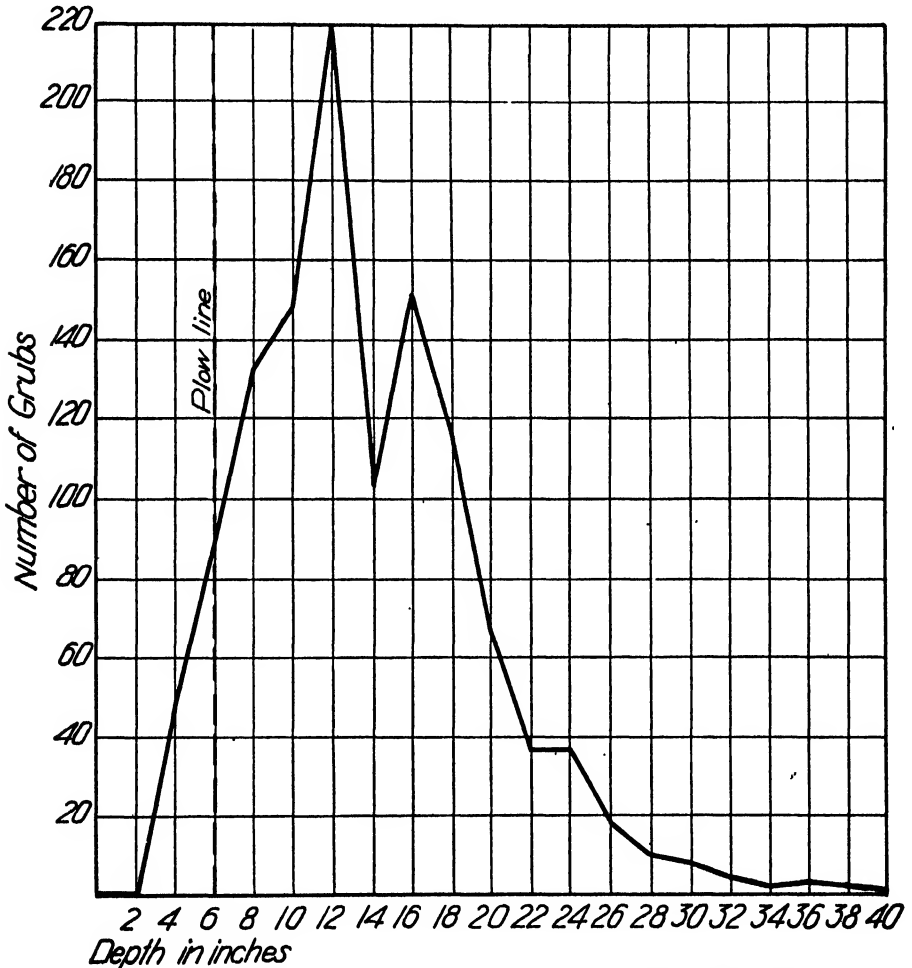


FIG. 1. Graph showing depth of collections of all grubs for five seasons.

greatest number (150) was found 12 inches deep, and the greatest depth from which a specimen was taken was 40 inches. The number of specimens taken at the various depths is shown graphically in Fig. 1.

It is also of interest to observe from Table I that the highest per cent of grubs found above the plow line for any year was 18.6, while the lowest was

8.6 per cent. It is apparent from a comparison of the graphs (FIG. 2) for the years 1922-1923 and 1925-1926 that the 12 inch depth is perhaps the optimum, or at least the safe depth for survival during the ordinary winter. In this connection it should be stated that a study of the soil temperature shows that it rarely fell as low as 32° F. at 12 inches below the surface.

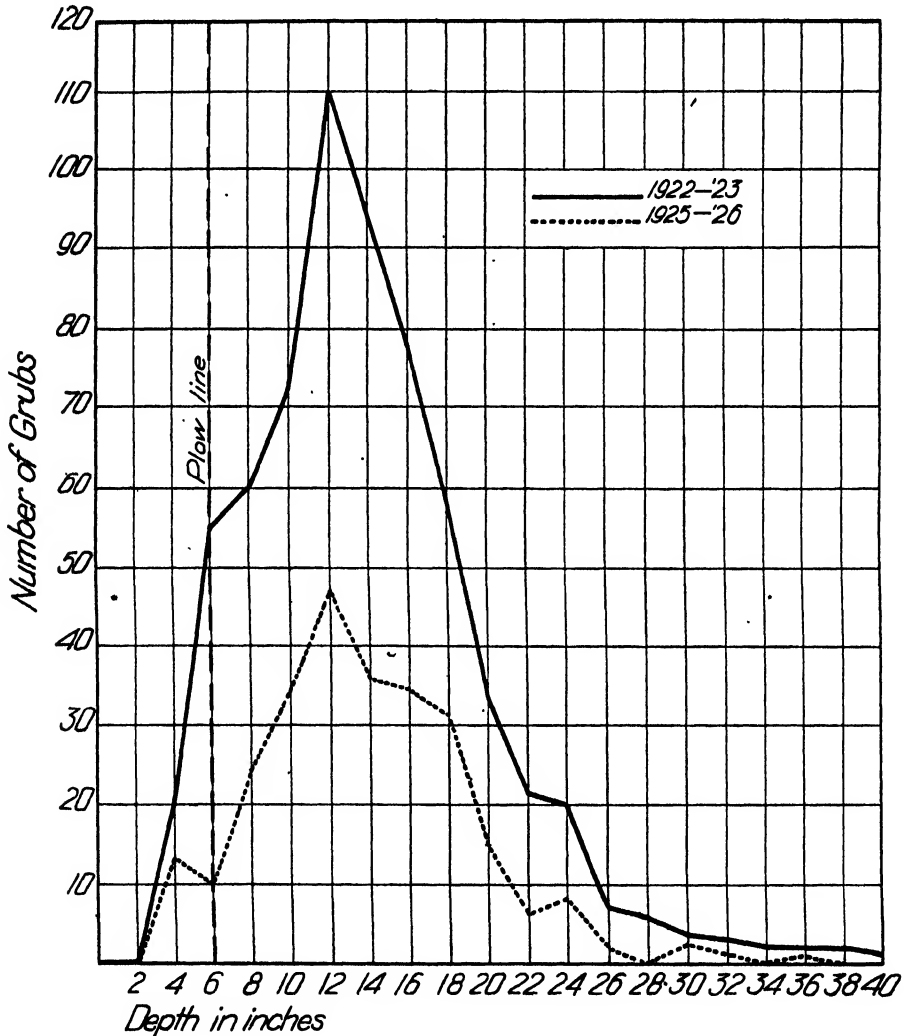


FIG. 2. Graph showing depth of collections of all grubs in 1922-1923, and 1925-1926.

An attempt was made to rear to the adult stage all grubs taken in this work. A summary of these rearings is presented in Table II, which shows the number of grubs of each species identified and the depths at which they

were taken. The data on *Phyllaphaga lanceolata*, which are incorporated in this table, were secured from a series of excavations in a wheat field at Goddard, Kansas, March 13, 1919.

TABLE II. *Summary of the depth of hibernation of white grubs*

Species	Total collected	Depth in Inches		
		Maximum	Minimum	Weighted Average
All white grubs	1,188	40	3	13.2
<i>Ochrosidia immaculata</i>	101	30	4	13.9
<i>Phyllophaga crassissima</i>	3	17	13	15.0
" <i>rugosa</i>	4	26	10	18.0
" <i>glabricula</i>	3	19	16	17.7
" <i>submucida</i>	1	14	14	14.0
" <i>rubiginosa</i>	1	14	14	14.0
" <i>bipartita</i>	1	15	15	15.0
" <i>corrosa</i>	1	16	16	16.0
" <i>lanceolata</i> *	66	20	3	10.3
<i>Anomala innubia</i>	99	15	4	8.9
" <i>ludoviciana</i>	2	30	20	25.0
<i>Diplotaxis</i> sp.	1	15	15	15.0
<i>Bolbocerosoma bruneri</i>	5	15	10	11.6

* Grubs collected at Goddard, Kansas.

Table II brings out the fact that the average depth of hibernation of all species was below the plow line. In fact, grubs of only two species were found above the 6 inch level in the work at Manhattan, while a few grubs of *Phyllophaga lanceolata* were taken at three to 6 inches at Goddard. While very few determinations were made of the grubs of *Phyllophaga* collected at Manhattan, it is interesting to note that all were several inches below the plow line.

Grubs of *Ochrosidia immaculata* predominated in practically all collections. Out of a total of 101 grubs of this species, only 12 were found above the plow line. The remaining 89 were found at depths ranging from 7 to 30 inches, with the majority at the 14 inch level.

In *Anomala innubia*, which ranked second in number of grubs identified, 99 specimens were taken. This species does not burrow downward to any great extent for hibernation. The average depth for it was 8.9 inches, with extremes of 4 and 15 inches. *Anomala ludoviciana*, on the other hand, apparently burrows deeply into the soil, as evidenced by the two specimens taken at depths of 20 and 30 inches.

Hibernation of Scarabæid Beetles

A total of 106 beetles, representing 15 species of the family Scarabæidæ, were collected during the course of these studies. The data relative to the depth of hibernation of the different species are summarized in Table III.

TABLE III. Summary of the depth of hibernation of Scarabæid beetles

Species	Total collected	Depth in inches		
		Maximum	Minimum	Weighted Average
<i>Phyllophaga rugosa</i>	22	20	4	12.6
" <i>rubiginosa</i>	18	18	2	9.9
" <i>crassissima</i>	14	9	2	5.4
" <i>hirticula</i> var. <i>comosa</i>	13	18	4	11.6
" <i>bipartita</i>	9	16	4	10.0
" <i>vehemens</i>	6	16	3	10.5
" <i>futilis</i>	2	12	5	8.5
" <i>fusca</i>	2	15	12	14.0
" <i>implicata</i>	1	10	10	10.0
<i>Ligyris gibbosus</i>	6	18	11	15.3
<i>Anomala binotata</i>	4	19	14	16.0
<i>Diplotaxis</i> sp.....	6	18	7	12.7
<i>Cotalpa lanigera</i>	1	15	15	15.0
<i>Pinotus carolina</i>	1	24	24	24.0
<i>Euphoria inda</i>	1	2	2	2.0

A comparison of Table III with Table II shows that, as a rule, the adults do not burrow as deeply as do the grubs. While the average depth of all species, except two, is below the plow line, it is interesting to note that the minimum depth for 9 species is less than 6 inches.

The data on the 9 species of *Phyllophaga* are of considerable interest. Most of the species of this genus transform to the adult stage in the autumn and, until recently, it has been supposed that the beetles passed the winter in the pupal cell. Criddle (loc. cit. footnote 2), however, has shown that the adults of certain species of *Phyllophaga* and allied genera migrate downward. He found adults of *P. rugosa* at an average depth of 20.5 inches, with extreme depths of 16 and 47 inches, while *P. nitida* was found only at depths of from 6 to 12 inches. The present studies confirm the work of Criddle and indicate that most species show a tendency to burrow several inches below the pupal cell for hibernation. *P. crassissima* was apparently the only species encountered which did not leave the pupal cell or at least did not migrate far below the place of pupation. The average depth of hibernation for this species was only 5.4 inches, with extremes of two and nine inches. *P. rubiginosa* was another species that frequently remained in its pupal cell. Of the 18 specimens collected, 6 were above the plow line and 3 others were just below it. The other species of *Phyllophaga* found in this study usually migrate downward, although an occasional beetle may remain in its pupal cell.

While the data on the other species of Scarabæids are rather meager, they indicate that, with the exception of *Euphoria inda*, the beetles burrow below the plow line for hibernation. Two of these species—*Ligyris gibbosus* and *Euphoria inda*—mature in late summer and are active for several weeks before going into hibernation.

Hibernation of Tiphia spp.

In connection with the work of digging for Scarabæid larvae and adults, some collecting was done of other insects found in the excavations. Among these were numerous cocoons of the black digger-wasps (*Tiphia* spp.), the larvae of which are commonly known to be important ectoparasites of the grubs of *Phyllophaga*, *Ligyris*, *Ochrosidia*, and related genera. Davis⁴ ('19), who has worked out the life-history of several species of *Phyllophaga*, states that most of them winter as larvae in the cocoons, but some species, of which the adults appear earlier in the summer, may winter as pupae.

When the ectoparasitic larvae of *Phyllophaga* are mature, the host dies and the *Tiphia* larvae spin a fluffy golden-brown cocoon in the cell of its host. These cocoons are from 15 to 25 mm. in length, depending on the species, and their frequent occurrence in the soil is ample evidence of the importance which they often assume in keeping down outbreaks of white grubs. Since they are often abundant and important, it is of some interest to know how deep they may be found in the soil during the winter.

The cocoons are stationary after having been spun, so empty cocoons, as well as those containing living insects, were collected. Naturally, they will be found at the point where the host died, and generally the exoskeleton of the larval host remains attached to the old cocoon. Collections were made throughout these studies, and the data obtained are summarized in Table IV.

TABLE IV. *Depth of hibernation of Tiphia spp.*

Depth (inches)	Winter of					Total
	1919-20	1920-21	1922-23	1923-24	1925-26	
Maximum.....	18	16	22	23	16	23
Minimum.....	4	8	2	13	6	2
Weighted Average.....	11.8	10.0	10.1	17.2	9.9	11.1
No. collected.....	8	10	51	14	20	103

From Table IV it will appear that *Tiphia* cocoons are found at depths ranging from 2 to 23 inches, with an average of approximately 11 inches. Whether or not the host larvae carry the parasites as deep as 23 inches, or the parasitic adults penetrate the soil to that depth in search of their host, is a matter for further investigation. It is important to note from these observations that the frequently recommended practice of fall plowing for white grub control will at the same time destroy those *Tiphia* cocoons which occur in the soil between 2 and 6 inches.

⁴ Davis, J. J. "Contributions to a knowledge of the natural enemies of *Phyllophaga*." Ill. Nat. Hist. Surv. Bull. XIII, Art. V, pp. 53-138, pls. 3-15, 1919.

Relation of Soil Temperature to Hibernation

A study of soil temperatures to a depth of 6 feet was made in connection with the investigations of hibernation, and a preliminary report of these studies is contained in a previous paper (McColloch and Hayes, loc. cit., footnote 3). The subsequent investigations confirm the results presented in that paper, and show that the reversals or "overturms" of temperature conditions in the soil occur at approximately the time when the downward (autumn) and upward (spring) migrations of the white grubs and May beetles take place.

It has also been found that at Manhattan, the soil seldom freezes below nine inches, and that on only a few occasions did the temperature at 12 inches fall as low as 32° F. Since the average depth of hibernation of practically all species of grubs and beetles was nine inches, or lower, it would seem that they burrow deeply enough to escape freezing conditions.

SUMMARY

The present study was made to ascertain the depths to which larval and adult Scarabeids penetrated the soil to pass the winter. The subject is of importance in making winter control recommendations, since it is necessary to correlate the winter habits of the insects with fall and winter farm operations. The study shows that in Kansas, 89 per cent of all grubs found were below six inches. It is further demonstrated that the grubs do not penetrate deeper than 40 inches, while the majority are between 6 and 20 inches. Where rearings were made after collection, it was possible to show the depth of penetration for the several species.

A study of the hibernation of adult beetles shows that, with the exception of *Pinotus carolina* which was found at 24 inches, adults of none of the species were taken as deep as were the larvae. The greatest depth at which an adult was taken was 20 inches for *P. rugosa*, which is considerably less than reported by Criddle (loc. cit., footnote 2) for similar species in Canada. It is of interest to note that Criddle found 20.5 inches to be the average depth of hibernation for *P. rugosa*, while in this study 20 inches was the maximum and four inches the minimum depth, with the majority of beetles at from 12 to 16 inches. In genera other than *Phyllophaga* (*Anomala*, *Diplotaxis*, *Ligyris*, *Cotalpa* and *Pinotus*), all adults found were below the plow line, with the single exception of a lone specimen of *Euphoria inda*, which was found 2 inches below the surface.

Included in this data are notes on the collection of *Tiphia* spp. cocoons, an important ectoparasitic enemy of white grubs, in which it is shown that these cocoons are normally found at an average of 11 inches in depth, with extremes of 2 and 23 inches.

A study of soil temperature in connection with these investigations indicates that most of the grubs and beetles burrow deeply enough to avoid freezing conditions.

RED SQUIRREL DAMAGE TO CONIFEROUS PLANTATIONS AND ITS RELATION TO CHANGING FOOD HABITS

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For several years a winter injury of unknown cause had been noticed in central Massachusetts coniferous plantations by members of the Harvard Forest staff. Twigs were cut off as cleanly as though by a knife, and in sufficient quantities to cause real damage to the trees. During the winter of 1924-25, a study of the injury was made.

To find the cause of the damage, several plantations were watched during early winter until, with the first heavy fall of snow, the clipping began. Then a plantation of Scotch pine (*Pinus silvestris*) where the activity appeared to be greatest, was watched from a blind until a red squirrel, *Sciurus hudsonicus loquax* Bangs¹ was seen doing the cutting. A study of the squirrel's habits here made it possible to identify him as the cause of all other fresh work found. He was also later seen eating European larch (*Larix europaea*) and white pine (*Pinus strobus*) buds.

The next objective was to find out from the forester's standpoint how serious the injuries were. The damage takes place only when it is difficult or impossible for the squirrel to find food on the ground. A period of warm weather following such a time and resulting in the thinning of the snow to a few inches in depth greatly reduces the amount of damage per day. An exception to this general statement is that European larch and white pine buds, at least, are eaten when they are just beginning to swell in the spring.

Scotch pine, Norway spruce (*Picea Abies*) and European larch are heavily injured. Only one red pine (*Pinus resinosa*) was found damaged out of hundreds examined. White pine is ordinarily immune, but in a winter of deep snow a heavy leader injury takes place. Often a group of young trees will be over ninety per cent injured, and in one case trees up to 25 feet tall lost their terminals. Red spruce (*Picea rubens*) is apparently ignored entirely. It was thought that white spruce (*Picea canadensis*), a species introduced from further north, but which grows vigorously in northern Massachusetts, would be strongly attacked. Examination of several hundred trees in a 19 year old plantation showed only one injury per hundred, while a nearby stand of Norway spruce was heavily damaged.

Besides the region where the study was made, the author has found the injury in northeastern Massachusetts, northern Connecticut and central New York. So it is by no means local, and probably occurs throughout the range

¹ Local variety determined by Robert T. Hatt.

of the two sub-species, *Sciurus hudsonicus loquax* Bangs and *Sciurus hudsonicus gymnicus* Bangs.

INJURY TO SCOTCH PINE (*Pinus silvestris*)

Scotch pine suffers most of any species studied. The large bud clusters seem to have a great attraction. The twigs are large and hard to cut. The buds are all in the end cluster, and so are usually cut off where the wood begins. The contents are cleaned out, and the split sheaths dropped down to litter the snow. A cluster of terminal buds is usually eaten clean (Fig. 1) leaving none to carry on normal height growth. Usually, at the same time, the topmost whorl of lateral branches and an occasional one lower down is clipped. The species has the ability of adventitious growth which causes a very characteristic form. Many of the terminal needle fascicles apparently form branchlets giving an enlarged, "broomed" appearance to the branch. A single injury can be outgrown, but the numerous branchlets get a fair start during one growing season and are often subjected to new injury the following winter. When this has been repeated for three or four successive years the production of good quality lumber by the tree is postponed if not prevented. The data on damage of 1924-25 could be easily recorded for different classes of injury, but earlier years were much more difficult to determine, so only "injured" and "uninjured" groups were made for the earlier season.

The winter of 1923-24 was one with a very high percentage of injury. Weather records taken at the Forest Headquarters show that from November 1 to March 31 the precipitation in 1923-24 was 4.3 inches more than in 1924-25 and 3.0 inches more than the average for the ten years ending with March 1925. As a contrast, the precipitation in the 1924-25 period was 1.2 inches below the ten year average. The data for the two winters from five plantations in Petersham, bring out the comparisons of resultant damage very clearly.

TABLE I. *Injury of 1923-24 in Pinus Silvestris; (heavy snow)*

Plantation Number	Area in Acres	Age in Years	No. Trees Examined	Percentage of trees injured	Percentage of trees uninjured
1	1.3	16	50	92	8
2	.6	15	50	90	10
3	.4	16	50	100*	—
4	.7	15	50	98**	2
5	1.0	14	100	86	14
Totals and averages...	4.0		300	93.2	6.8

* 1922-23 injury 100 per cent, not included in that for 1923-24.

** 1922-23 injury 82 per cent, not included in that for 1923-24.

TABLE II. *Injury of 1924-25 Pinus silvestris; (below normal snowfall)*

Plantation Number	Percentages				
	Part of Tree Injured			Total Injured	Total Uninjured
	Terminal Only	Terminal and Laterals	Laterals Only		
1	4	14	6	24	76
2	—	82	8	90	10
3	2	84	8	94	6
4	2	66	2	70	30
5	—	—	—	—	100
Averages	1.6	49.2	4.8	55.6	44.4

INJURY TO NORWAY SPRUCE (*Picea Abies*)

The bud arrangement on Norway spruce twigs leads to a different method of attack from that in Scotch pine. The terminal bud is well armored by many sharp, forward-pointing, stiff needles and cannot well be eaten from the end, so a cut is made at the base; the green tissue is taken out and the bud sheath is left looking so nearly normal that it would not often be noticed as damaged by one not familiar with the injury. These end buds are sometimes all that are touched on the branch, but the lateral ones near the tip usually suffer also. They are like small, fat brussels sprouts and make very easy feeding for the squirrel. A twig or leader tip a few inches long carries several of these buds. Apparently to save effort, a twig is cut off from one-half to five inches back from the end and taken to a point on a larger branch where it can be wedged among the thick needles and the contents of the buds hollowed out (Fig. 2). Often dozens of these rifled tips can be found in one tree. The cutting does not seem to be confined to any one part of the tree. In larger specimens, where the leaders have reached a diameter of three-quarters of an inch or more, the buds usually are untouched. Where the leaders are small they are riddled and most of the lateral branches having sizeable buds are given the same treatment on all trees alike (Fig. 3). Only slow-growing or unhealthy trees with small buds escape.

Recovery from the injury is more rapid and more successful than in Scotch pine. The strong, centralized, upward growth from lateral buds left untouched soon replaces the leader. Usually only one good shoot results, and this straightens out at the point of injury so well that in a year's time the only evidence of the damage is the dead stub of the former leader protruding at a point where there is a slight crook. As wood is laid on for a few years over this section, the crook largely disappears. Lateral branches never make any further growth at the injured tips.

The comparative amounts of injury in the two winters studied is shown in the following tables covering four areas in Petersham and one in Clinton, Massachusetts. The same trees were used for the different years.

TABLE III. *Injury of 1923-24, Picea Abies*

Plantation Number	Area in Acres	Age in Years	No. trees examined	Percentage of trees injured	Percentage of trees uninjured
1	2.4	14	50	74*	26
2	2.9	11	50	64†	36
3	.1	16	50	96‡	4
4	1.0	16	50	32	68
5	2.0	19	100	75	25
Totals and averages . .	8.4		300	68.2	31.8

* 1922-23 injury 64 per cent, not included in that for 1923-24.

† 1922-23 injury 44 per cent, not included in that for 1923-24.

‡ 1922-23 injury 90 per cent, not included in that for 1923-24.

TABLE IV. *Injury of 1924-25 Picea Abies*

Percentages

Plantation Number	Part of Tree Injured			Total Injured	Total Uninjured
	Terminal Only	Terminal and Laterals	Laterals Only		
1	—	—	—	—	100
2	—	—	—	—	100
3	—	24	34	58	42
4	—	—	—	—	100
5	—	8	49	57	43
Averages	0	6.4	16.6	23	77

INJURY TO EUROPEAN LARCH (*Larix europaea*)

The injury in European larch of the sizes available for study (12-29 feet tall) is one of lateral bud eating only. There are two types of work. One takes off the small twigs which grow in great numbers from the main stem. The other takes the tips from the large limbs. A rather long section is cut off in either case. Fifty cuttings picked at random gave an average length of 10.9 inches. They are, of course, very light and slender. The buds are small, and those on new growth are eaten from the tip end. On year-old branches they are usually cut in from the side to remove the contents. The twigs are dropped to the snow at the base of the tree (Fig. 4) and in summer the accumulation from two or three years' work often forms a thick mat.

When the buds are just beginning to show growth in the spring, a second session of damage occurs, but the buds only are removed, leaving the twigs intact.

Only very severe cases of damage seem appreciably to retard the growth of the trees. When a stem is clipped up to almost a bare pole it, of course, can make little growth. This is, however, exceptional, and recovery usually seems well under way the first season.

That larch is not as eagerly eaten as Scotch pine is evidenced by the fact that in adjoining, nearly equal-aged plantations of the two species, larch show no injury during 1924-25 while 90 per cent of the pines were attacked.

Nine plantations covering 4.0 acres were studied, and only two of these were damaged in a rather spotty way during the time of observation, although each had been thoroughly attacked in previous winters. No representative figures on the amount of damage could be gotten from these. Data on past injury is very hard to obtain because the rapid growth from cut twigs makes determination of the year of injury little more than guesswork. The twigs dropped to the ground are of no greater help, because they are often mixed with those left by rabbits gnawing at lower limbs and by porcupines working higher up. The buds go to pieces quickly, and after they are gone it is impossible to tell whether the work was done by squirrels or not.

DAMAGE OF 1925-26

No data on the amount of the injury during 1925-26 were taken, but several plantations of the three injured species were under observation during the period of deep snow. While the precipitation from November first to April first was only .3 inch greater than in the same part of 1924-25, and .87 inch less than the ten year average mentioned above, the snow lay from two to six feet deep in the plantations for an unusually long, unbroken period.

The damage was heavier by far than in either of the two previous winters. It was carried uniformly over all the trees, and practically all sizeable, lateral branches as well as the terminals of the spruce and pine were budded.

CHANGING FOOD HABITS A POSSIBLE CAUSE OF THE INJURY

Why the squirrel did not damage plantations until recent years is a question naturally arising in the course of the study. Biologists tell us that something of real importance must happen to change the feeding habits of an animal over a considerable area. The squirrel is not limited in travel to a small circle surrounding his nest, as is evidenced by the fact that in one of the spruce plantations studied the injury was carried uniformly out to the edge which was six hundred feet from the nearest forest cover. Paulmier² claims that squirrels have been known to cross a lake during the fall in search of a good crop of chestnuts. This response to food supply seems to explain the limiting of the injury to recent years. The original, old-growth, mixed forest contained large trees that bore a variety of squirrel foods. The pines were old enough to bear cones in abundance. The oak, beech and chestnut furnished such a quantity of mast that pigs could be fattened on it. This condition has been radically changed. Logging has left in place of the old pines only young ones bearing relatively few cones, many of which never mature due to insect infestations. Areas denuded of their mast-bearing hard-

² Paulmier, Frederic C. "The squirrels and other rodents of the Adirondacks." Report of the Conservation Commission of New York. 1902-03.

woods have seeded in to species whose winged seeds are easily wind blown. Only an occasional oak or beech too young to bear fruit is found among them. The chestnut, a great food producer of former years, is so completely wiped out by the blight that a nut-bearing tree is a rarity in this region. The present day cut-over land has a growth in which squirrel food during the spring and summer is abundant, but in which supplies for winter storing are very hard to find. The result seems obvious. The coniferous plantations whose large buds are eatable offers a good emergency ration when the snow's depth prevents finding food on the ground. This behavior is not from preference but from necessity. That natural winter food obtainable through the snow will result in comparative freedom from injury in nearby plantations seems to be indicated by one area studied.

About two acres of thirteen year old Norway spruce were examined very carefully. Not a single injury was found until the winter of 1925-26 when a large percentage of the leaders were nipped off. The stand was one such as had invariably been found to be damaged year after year in other locations. There were many squirrels about, so the reason for the comparative immunity appeared to be that the animal's habits here differed from those of the ones around the other plantations. All the repeatedly damaged areas were surrounded for a considerable distance by young stands of white pine and hardwood. Near this area which came so near escaping were acres of old-growth pine, hemlock and hardwood up to a hundred years or more in age. Quantities of pine cones, acorns and beechnuts were available for fall storing, this being one of the few local sections where gray squirrels are still found. Apparently it took a winter when the snow was several feet deep for weeks at a time to make the normal food supply fail. This seems to show that the injury in plantations near similar old-growth is only occasional if not entirely lacking.

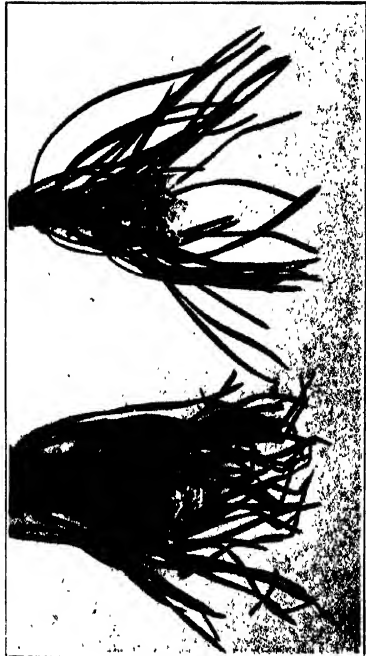
SUMMARY

During periods of deep snow when the red squirrel's usual food supply is cut off, it eats the buds of certain coniferous trees, the normal growth of which is thereby retarded. Scotch pine terminal and lateral buds, Norway spruce terminal buds and lateral branch tips, European larch lateral branch-ends, and white pine terminal shoots are clipped off. Scotch pine apparently suffers most, with Norway spruce and white pine close behind. European larch recovers well from the injury.

The intensity of the injury varies directly with the depth of the snow and the length of time it remains between thaws.

The damage has been found by the author in three states, and so is not local.

The fact that the damage has been apparent only in recent years seems to be explained by the lack of pine seed and hardwood mast for winter storing which are less abundant in the present young, cut-over forests of light-seeded species, from which, furthermore, the chestnut has completely disappeared as a source of food.



1



2



3



4

PLATE V. 1. Normal and budded Scotch pine leaders. 2. Norway spruce tips with rilled buds. 3. Norway spruce branch clipping. 4. European larch twigs dropped on the snow after buds were eaten.

EXPERIMENTAL FEEDING OF OYSTERS¹

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Three theories have been advanced as to the nature of the fundamental food of oysters and other bottom-feeding invertebrates. The oldest view is that the plankton organisms constitute the principal source of nourishment of these animals and that food derived from other sources is relatively unimportant. This is the view avowedly or tacitly held by practically all of the earlier students of the subject, and, although it has been attacked in recent years, it has found support from Nelson ('23, '25b), Hunt ('25) and myself (Martin '23) among others, and especially from Yonge ('26). The attacks have been mainly from the supporters of an opposing theory who maintain that the fundamental food of these animals is the dust-fine detritus derived from the comminution of the larger plants, particularly *Zostera*, and that the plankton organisms play a subordinate role, mainly through the addition of their dead bodies to the mass of detritus. This view, first suggested by Petersen, and Petersen and Jensen and greatly elaborated by Blegvad, has been vigorously supported in recent years by Spärck ('25) although in his later papers ('27a, '27b) Spärck withdraws very materially from the extreme views expressed in his earlier publication.

A third theory has been advanced, namely, that many marine animals, including vertebrates as well as invertebrates, may utilize dissolved organic materials directly. As originally proposed in extreme form by Pütter ('09) it has been shown to be untenable. Churchill ('16) showed experimentally that fresh water mussels may utilize organic substances in this way, although as Yonge points out, it may have been indirectly. Churchill and Lewis ('24) admit that they probably do not form a very important item in the dietary of lamellibranchs under natural conditions. The other evidence which has been advanced as favoring this hypothesis can better be explained by the plankton theory.

The earlier literature has been summarized in a number of recent papers (Martin, '23, Churchill and Lewis, '24, Savage, '25, Yonge, '26, Martin, '27a), and detailed mention need here be made of a few recent studies only.

Spärck, in his 1925 paper, regards it as proved that detritus is always the main food of the European oyster, although he cites one instance, which he regards as exceptional, in which *Prorocentrum micans* seemed to be the main source of food. He adds, as has been noted by other workers, that this or-

¹ Publication No. 12, New Jersey Oyster Investigation Laboratory.

ganism as well as diatoms may pass through the digestive tract uninjured. The fallacy of deducing from this that the oyster is unable to utilize these forms is pointed out by Nelson ('25a). Spärck cites the fact that certain oysters had only "a greenish mass of detritus" in their stomachs as evidence that they were not feeding on organisms. In this connection I have recently pointed out ('27b) that the zoospores of *Enteromorpha* very quickly after ingestion form an amorphous mass which would ordinarily be classed as detritus, and unpublished observations by Nelson and myself show that the same thing is true of other naked organisms, hence it is probable that much that has heretofore been found in the stomachs and classed as detritus is really material taken by the oyster as living plankton.

Dodgson ('16-'26) in a series of informal reports shows conclusively that nanno-plankton organisms, and particularly a small species of *Chlorella*, may be an important source of oyster food in England. Hunt ('25), in a comprehensive study of the food of the bottom fauna, regards the microflora as the important source of detritus in the region studied. While oysters were not included among the animals he studied, it seems clear that they would fall into his category "suspension feeders" living on microplankton forms and detritus derived from these. Savage ('25), while he does not reject the detritus theory, believes microorganisms are of greater importance than the Danish workers have been willing to admit. Yonge ('26) shows that oysters are particularly adapted to assimilate microorganisms rich in carbohydrates, such as diatoms and peridines, the forms with hard walls being digested by phagocytes. In his 1927 papers, Spärck, in marked contrast with his previous views, admits that it may be regarded as proved that oysters are able to feed exclusively on microorganisms, and that in certain natural localities these may constitute their main or even their sole food. He suggests that detritus may be used indirectly, through the agency of endozoic microorganisms, but offers no proof that this actually takes place. He also finds that oyster larvae feed neither on detritus nor on dissolved organic substances, but on very small green organisms, a species about 3μ in diameter being especially favorable, thus confirming the observations of Hori ('26) and Amemiya ('27).

During the summer of 1925 some experiments were conducted in New Jersey (Martin '27a) which showed that it was possible to feed young oysters pure cultures of selected organisms in relatively small quantities of water, and get them to grow. In three weeks different lots of oysters fed in this way gained from 4.7 per cent to 11.1 per cent in average shell diameter, while starved checks made a gain of only 2.7 per cent. The greatest gain, 11.1 per cent, was made by the lot fed on the diatom *Amphora coffeaeformis* var. *lineata*; the lot fed on the alga *Gloeocystis vesiculosa* gained 9.7 per cent; those fed on scraped *Zostera*, representing detritus, gained only 6.4 per cent. This was interpreted as proving that the oysters could and did assimilate the diatom and alga to better advantage than the detritus. During the same time

oysters kept in an enclosed basin and allowed to feed on the rich plankton there, gained 45.2 per cent, suggesting that conditions in the experimental jars were much below optimum. It seemed desirable to repeat this work with certain modifications suggested by the first attempt. The experiment was conducted as before on the houseboat laboratory of the Department of Biology of the New Jersey Agricultural Experiment Station, moored during the summer of 1927 near Bayville, on the west side of Barnegat Bay. The location was in a small creek connecting the Bay with a shallow brackish pond very rich in plankton. The jars and stirring apparatus were the same ones used in the 1925 experiment, but driven by a larger and more dependable motor. Power was supplied by a Homelite portable electric plant, operating on furnace oil. The stirring apparatus was operated for from ten to twelve hours during the day, this proving sufficient to aerate the water so that its alkalinity remained fairly constant, ranging between pH 7.8 and pH 8.2, which agreed very closely with the water in the creek and Bay where oysters were living naturally. Most of the material stayed in suspension fairly well even when the water was not being stirred. The diatom *Amphora coffeaeformis* did not, however, the clumps tending to fall to the bottom, and the same thing was true of the detritus, but not of all the organisms, composing the plankton, added to Jar 7. The attempt to secure spat in Barnegat Bay failed, but through the kindness of Mr. J. R. Nelson, spat was secured from Delaware Bay. This was mostly on glass slides but as there were not quite enough of these, some spat on shells were used, one shell or shell fragment being placed in each jar. The jars were square battery jars measuring ten centimeters in each dimension. Into each was poured about 750 cubic centimeters of the filtered water, and food was added as follows:

Jar 1. *Nitzschia paleaceae* Grun. A pure culture, grown in Allen and Nelson's solution and derived from the culture used in 1925. Individuals separate, and staying in suspension well.

Jar 2. *Amphora coffeaeformis* (Ag.) Kütz. A pure culture, grown in Allen and Nelson's solution and derived from the culture used in 1925. It massed in gelatinous clusters and quickly dropped to the bottom when the water was still.

Jar 3. *Chlorella* sp. A pure culture in Allen and Nelson's solution. This is the organism noted by Dodgson as important in fattening oysters in England, and sent from there to Dr. T. C. Nelson through the courtesy of Dr. Dodgson. This organism stayed in suspension all the time, and after its first introduction into the jar increased so rapidly that there was some danger of overabundance, hence at one time during the experiment about two-thirds of the water in the jar was siphoned off and replaced with centrifuged water.

Jar 4. *Gloeocystis vesiculosa* Nägeli. A pure culture in Allen and Nelson's solution, derived from the culture used in 1925.

Jar 5. An unidentified naked brown flagellate isolated from an old cul-

ture of Bay water and grown in Allen and Nelson's solution. It is oval or irregularly pyriform in shape, with two flagella and a beak-like projection at the anterior end, the body measuring $6-7.5 \times 3.5-4.5 \mu$. It tended to accumulate at the top of the jar and toward the better lighted side.

Jar 6. Yeast. Isolated from a Fleischmann's yeast cake and grown on nutrient agar. The cells tended to sink to the bottom when the water was quiet.

Jar 7. Plankton. Secured from the creek and concentrated by hand and power centrifuges. It contained a wide variety of organisms and at times a great deal of detritus, and colloidal matter which would be classed as detritus. The detritus elements and most of the organisms tended to sink rapidly to the bottom when the water was not being agitated.

Jar 8. Check. Not fed.

In addition, a small lot of spat was put in a jar and placed on a platform in the brackish pond near the houseboat, about a foot above the bottom and with the mouth from three or four inches to a foot or more under the surface, according to the tide.

The water placed in the jars at the beginning was filtered through fine filter paper and when tested by centrifuging proved to be practically barren. It was, of course, impossible to avoid introducing some organisms with the oysters, and after the oysters were removed at the end of the experiment, the water in each jar was examined to find out to what extent foreign organisms had multiplied, with the following results:

Jar 1. *Nitzschia*. Cells abundant and in suspension. Few foreign organisms present.

Jar 2. *Amphora*. No cells in suspension and comparatively few in the detritus on the bottom of the jar. A few small worms (*Nereis*) present and many ciliate protozoa.

Jar 3. *Chlorella*. Many cells in suspension and on bottom at end of experiment, also some *Gloeocystis* cells. A few nematodes in the bottom of the jar and a number of colonies of a fungus belonging to the genus *Cladosporium* and producing spores abundantly.

Jar 4. *Gloeocystis*. Abundant in suspension and on bottom. Very few foreign organisms present.

Jar 5. Brown flagellate. Abundant in suspension. A few *Gloeocystis* cells also present. Some small diatoms, mostly *Nitzschia palea*, on bottom.

Jar 6. Yeast. None in suspension, but a few green flagellates present. Yeast cells abundant on bottom, many partly disorganized. Numerous amoeboid and flagellate protozoa and many bacteria on bottom.

Jar 7. Plankton. Almost nothing in suspension. Bottom thick with detritus, in which were a number of small diatoms and colorless ciliates.

Jar 8. Starved. Nothing in suspension. Scanty detritus at bottom composed of dust and foeces. This material contained a few minute protozoans and some bacteria.

In cleaning the slides and shells and removing spat too close to each other, a certain amount of injury was done to some of the remaining oysters. This accounts for the different numbers in the various jars, since the records are based only on the oysters surviving uninjured to the end of the experiment.

The oysters were carefully measured at the beginning and end of the experiment, using a screw micrometer and reading the dorso-ventral and antero-posterior diameters to a tenth of a millimeter. The average of the two dimensions for the lot in a given jar was taken, and the gain expressed as a percentage of the original average diameter. No attempt was made to measure the food added, but an abundant supply was at all times present in all of the jars.

The experiment was started on August 14th and ran for fifteen days. The following table summarizes the results.

TABLE I. *Gain in size of oysters receiving different kinds of food*

Jar	No. of oysters		Av. diam. in mm. at beginning	Av. diam. in mm. at end	[Av. gain in mm.	% gain
1	14	Nitzschia.....	2.39	2.74	0.35	14.6
2	16	Amphora.....	3.02	3.65	0.63	20.9
3	14	Chlorella.....	2.54	3.07	0.53	20.9
4	16	Gloeocystis.....	3.05	3.96	0.91	29.8
5	14	Brown flagellate....	3.03	3.93	0.90	29.7
6	11	Yeast.....	3.04	3.74	0.70	23.0
7	13	Plankton.....	3.19	4.16	0.97	30.4
8	14	Check (starved)....	3.24	3.65	0.41	12.7
	8	Controls in pond....	3.47	9.37	5.90	170.0

In comparing these gains, made in fifteen days, with those made in 1925 in three weeks, it will be noted that the gains are throughout much greater, ranging from 12.7 per cent in the case of the starved oysters to 170 per cent in the case of the controls, as compared with 2.7 per cent and 45.2 per cent respectively in the earlier experiment. This may be accounted for by two factors: first, the oysters were much smaller to start with in 1927, hence the gain in diameter was more apparent; and second, there was at all times an abundant supply of food in the later experiment, while this was not always the case in the earlier one. The oysters were much more nearly uniform in size in the later experiment, thus minimizing one source of error. It remains true, however, that the results are in close agreement with those secured in 1925. Thus the oysters exposed to a natural environment rich in plankton organisms made far more growth than any in the experimental jars. The poorest growth was made by the starved oysters, and what gain was made was very thin, sometimes a mere film on the substratum. Of the two diatoms, the *Amphora* was the better in spite of its inability to stay in suspension. This may have been due partly to its smaller size (average length $12.5\ \mu$ as com-

pared with over 40μ for the *Nitzschia*) and partly to the numerous protozoa that it supported. That the latter may be the more important factor is suggested by the similar gain made by the oysters fed with yeast in Jar 6, where many protozoa and bacteria also appeared. In the series of pure culture feedings, the best gains were made by the oysters fed with small naked forms, particularly by the *Gloeocystis* and the brown flagellate, in which cases the gains were not significantly less than those made by the lot receiving the plankton and detritus. These results serve as additional evidence that oysters can and do utilize plankton organisms, especially the naked forms, and that the presence or absence of detritus in their food is of no direct importance.

SUMMARY

Small oysters were kept in battery jars under controlled conditions and fed various substances. Two jars received diatoms, (*Amphora* and *Nitzschia*); two, small non-motile algae (*Chlorella*, *Gloeocystis*); one, a small naked, brown flagellate; one, yeast, all from pure cultures. One jar received plankton and detritus concentrated by centrifuge; one jar received no food. The growth was measured by comparing the average diameter of all the oysters in each jar at the beginning and end of the experiment, expressing the gain as a percentage of the original diameter. The oysters fed plankton made the greatest gain, but this was practically equalled by those fed pure cultures of the brown flagellate and of the *Gloeocystis*. Controls kept in their natural environment made far better growth than any in the experimental jars.

It is concluded that oysters can make substantial growth on pure cultures of plankton organisms, and the results are held to support the contention of Yonge and others that there is no proof that they are able to utilize detritus directly.

I wish to express my indebtedness to Prof. T. C. Nelson for his cordial cooperation and valuable criticism during the course of this work.

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INFLUENCE OF SPHAGNUM AND OTHER MOSSES ON BOG REACTIONS

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PURPOSE

In this work the writer has attempted to show: (1) the influence of sphagnum and other mosses on bog reactions; (2) the minor rôle of sphagnum in the development of some so-called sphagnum bogs; (3) and incidentally the effect of hydrogen ion concentration on the distribution of certain bog plants.

METHOD

In all cases except the Hartford bog the samples from the deeper horizons were taken with a Davis peat sampler described by Dachnowski ('24). Dr. Hugo Oswald of Sweden, using a very efficient Swedish instrument, furnished the writer with samples of the Hartford bog. The hydrogen ion concentrations were determined by the colorimetric method as described by Clark ('20) and Wherry ('22), using color standards for comparison. The sphagnum content of the substratum was ascertained by microscopic examinations of the peat samples in the laboratory.

PRESENTATION OF DATA

Profiles, pH.—The data are presented in diagrammatic profiles, the younger zones being placed to the left. Excepting the Wauconda and Hartford bogs, concerning which see the text, the total depth bored for samples is to be found at one of the peat columns so that the value of the scale divisions will be obvious. The Cowles and Hartford bog profiles show peat legends. Exceptional soils like muck or pine needles are specially indicated. The moss indicated in the profiles is usually some member of the *Hypnaceae*, like *Amblystegium riparium* L., *Drepanocladus aduncus* (Hedw.) Warnst. or *Stereodon pratensis* (Koch.) Limbd. The pH may be read at the successive horizons beside the peat columns.

Listing of species.—Only species characteristic, important, or known to the writer are listed. The nomenclature is sometimes abbreviated. Sometimes only the generic name is given, for example "*Rhus*" ("*Vernix*," understood), or *Liriodendron*, which is monotypic.

Classification of habitats.—For reasons more fully developed in the discussion, the writer has classified the habitats studied under two headings,

namely "acid bogs" and "circumneutral bogs," according to the prevailing reactions.

ACID BOGS

Sayer Sphagnum Bog

Sayer bog, Wauconda bog, County Line Tamarack Forest, and Cedar Lake bog are among the Lake County, Illinois bogs located and described by Waterman ('26). The instrument had to be plunged in repeatedly before layers were struck where the sphagnum peat was disintegrated and compacted enough to be cut and retained by the sampler. Therefore a few unavoidable gaps occur in the data. Nevertheless, one sees a definite correlation between high acidity and presence of sphagnum. For instance at the pioneer *Typha latifolia*-*Aspidium thelypteris* zone the pH is 6.5; while only a few feet away

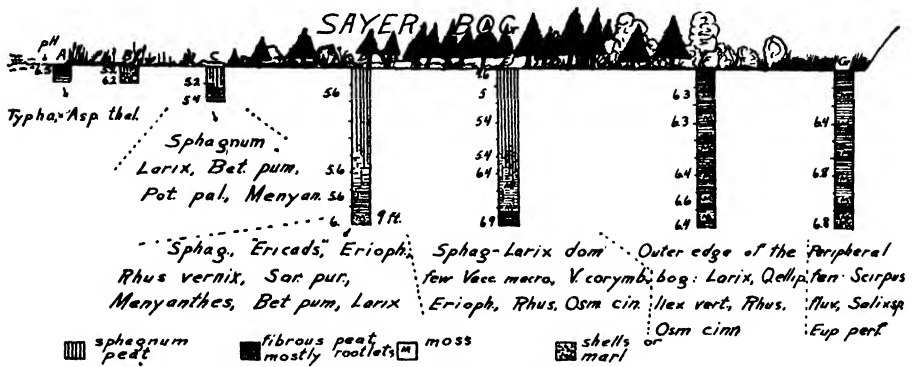


FIG. 1. Sayer Bog.

at the *Sphagnum cymbifolium*, Ehrh., frontier it drops to 5.2. From "B" on, the high acidity is maintained in the upper strata, reaching its maximum at "E." Neutrality is once more approached at "F" and the peripheral fen "G" where sphagnum is again absent. The correlation between high acidity and sphagnum is even more apparent in the substratum. "B," "C," "D" and "E" show that high acidity does not extend any appreciable depth beyond the sphagnum.

Hartford Sphagnum Bog

The Hartford sphagnum bog is at its best on the west end of a small lake located on State Highway 17, three miles east of Hartford, Michigan.

Decodon verticillatus, *Woodwardia virginica* and *Typha latifolia* are the pioneer mat formers. Next comes the sphagnum mat mostly *S. cymbifolium* Ehrh. and some *S. acutifolium* Ehrh. with *Acer rubrum*, *Larix laricina*, *Salix pedicellaris*, *Andromeda glaucophylla*, *Chamaedaphne calyculata*, *Sarracenia purpurea*, *Eriophorum virginicum*, *Potentilla palustris*, *Menyanthes trifoliata*, *Habenaria ciliaris*, *H. blephariglottis*, etc.

Under the tamaracks and pines are local colonies of *Sphagnum cym-bifolium* Ehrh. in more or less direct continuity with the underlying peat. These colonies are "relicts"; not all similar colonies are, as will be seen

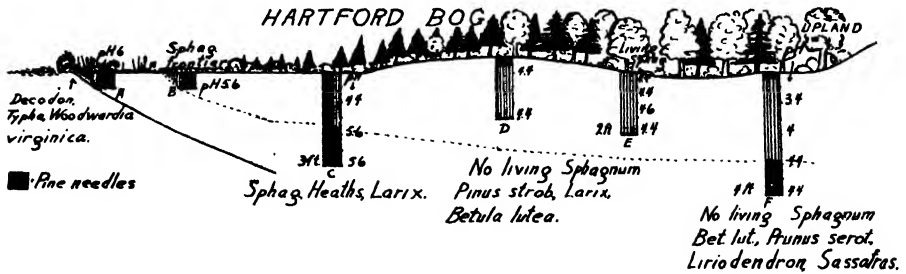


FIG. 2. Hartford Bog.

later. From the pine zone, samples were tested from successive horizons down to 9 meters—almost to the bottom, for at the sphagnum zone the sandy substratum was reached at about 8 meters. The peats, classified according to Dr. Hugo Oswald's field observations, showed the following reactions: 1.5 m., *Sphagnum* peat pH 4.0; 3.0 m., *Sphagnum-Carex* peat, pH 5.4; 4.0 m., *Carex* peat, pH 5.4; 5.0 m., *Carex* peat, pH 5.8; 6.0 m., *Drepanocladus* peat, pH 6.0; 7.0 m., mostly water, no test; 8.0 m., lake mud, pH 8.4; and 9.0 m., lake mud, pH 7.4. This profile study again demonstrates the importance of sphagnum as an acidifier of bogs. We find here, as at the Sayer sphagnum bog, a diminution of acidity, both laterally and vertically away from the sphagnum. The well preserved peat and the various zones almost lockstepping each other in orderly succession offer an excellent opportunity for an intensive study and comparison of vertical and horizontal zones.

Merrillville White Pine Sphagnum Bog

The Merrillville White Pine Sphagnum Bog is an old bog which has closed in over a small morainic lake, and is on the Indiana State Highway No. 2 about three miles east of Merrillville. Near the center there remains a small area, about 25 feet across where the sphagnum-heath association which has replaced the mat pioneer is in turn making its last stand. The loose and tough sphagnum peat made substratum samples unavailable here. Nothing is known, therefore, about the kind of peat or reaction below a foot. Down to a foot, however, the reaction was pH 5., and the peat, sphagnum.

This bog differs from the preceding two in that the once presumably non-sphagnous circumneutral pioneer mat has been completely superseded by a sphagnous acid mat. The oldest zone of this bog is dominated by a *Pinus strobus* association with no trace of *Larix*—in itself unique, since the latter does occur at Cowles bog about 10 miles away. *Rhus vernix*, *Osmunda cinnemomea* and *Woodwardia virginica* form most of the undergrowth. Here

the peat also proved to be too wet, loose and tough for an adequate number of samples. Nevertheless, a few samples obtained at random disclosed the presence of sphagnum and a high acidity (pH 4.0 to 5.0) down to at least 4 feet.

In the peripheral fen characterized by *Rosa caroliniana*, *Spirea tomentosa*, *Aspidium thelypteris*, *Eupatorium perfoliata*, *Alisma plantago*, and *Lycopus americana*, samples of non-sphagnum peat were taken to a depth of 12 feet. The pH for the surface was 5.8; three feet down pH 6.4; six feet pH 6.6; and at nine and twelve feet it was 6.8, almost neutral. Even the scant data for this bog show the rôle of sphagnum in acidifying bogs.

Cedar Lake Sphagnum Bog

The pH of sphagnum.—The foregoing sphagnum bogs are well marked by mature clear-cut acid sphagnum-heath zones. Cedar Lake described by Emerson ('21) and Waterman ('26) on the other hand, contains a relatively young mat with incipient colonization by *Sphagnum acutifolium* Ehrh. Higher acidity marks the very local sphagnum patches. A distance of only a few feet laterally from sphagnum is sufficient to lower the acidity by .5. Vertically the lowering of acidity is still more abrupt; it is diminished in a few inches from pH 4.0 to pH 7.5.

The pH of Mosses—Higher acidity is here also tied up with at least two other mosses. The reaction of a hummock of *Stereodon pratensis* (Koch) Lindb. was pH 4.6, while 5 inches below the bog water read pH 7.0. *Aulacomnium palustre* Schwaegr. gave more striking and complete data. Tests made on the living tops and peat of this moss showed reactions running from pH 4.4 to pH 7.3 depending on the proximity and abundance of the alkaline

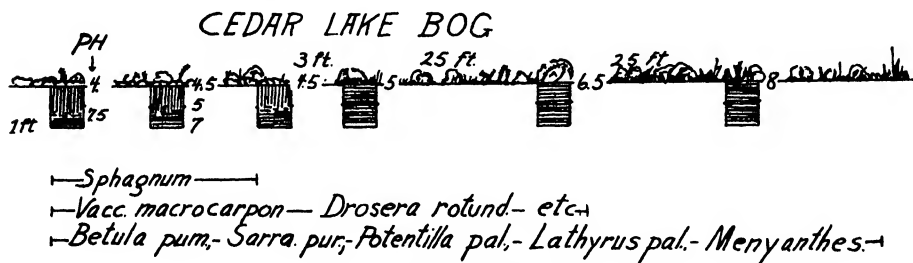


FIG. 3. Cedar Lake Bog.

or neutral water surrounding or underneath. In most cases the unbathed tops and peat of this moss showed reactions of pH 4.4, 4.5, and 4.6. *Aulacomnium palustre* Schwaegr. forms rather extensive mats wherein cranberries and sundews flourish. It will be seen therefore that this moss is here an important acidifier. Since this moss does grow in even alkaline waters one naturally wonders if it helps the establishment of sphagnum. It may; but

it is not a necessary forerunner because sphagnum is too often found within a few inches of a circumneutral substratum where *Aulacomnium palustre* Schwaegr. is absent.

CIRCUMNEUTRAL BOGS

Duck Lake Bog

The Duck Lake bog on the southern limits of Ingleside, Lake County, Illinois, was examined in the summer of 1922. The mat contained a number of so-called bog plants like *Sarracenia purpurea*, *Potentilla palustris*, *Menyanthes trifoliata*, *Lathyrus palustris*, *Parnassia caroliniana*, *Betula pumila*, *Salix pedicularis*, *S. candida*, and *Decodon verticillatus* near the water. Six tests about six inches deep in the younger unstable mat gave an average reaction of pH 6.5. In the more stable zone the average of four tests was pH 7.5. This circumneutral non-sphagnum bog, devoid of heaths and tamaracks, may be regarded as a typical fen. See Discussion.

Cowles Bog

Cowles Bog at the inlandward edge of the Lake Michigan dunes near Mineral Springs, Indiana, Baroda Bog near Baroda, Michigan, and Chesterton Bog near Chesterton, Indiana, are briefly discussed in a former paper, Kurz ('23). Subsequent microscopic examination of the peat, however, shed new light on their history.

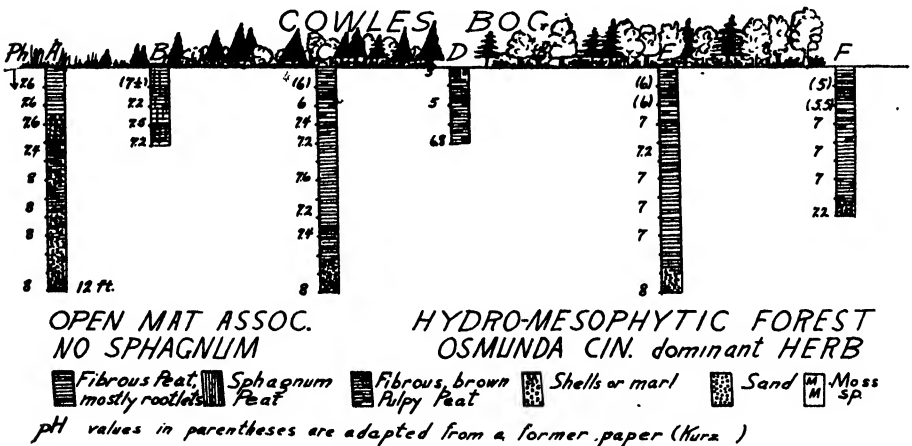


FIG. 4. Cowles Bog.

Cowles bog, although alkaline in the open mat, becomes acid in the older forested portion despite the sparse and very local development of sphagnum. The cause of acid in this case must therefore be linked up with other factors. A few studies made of the *Osmundas* suggest that the root excreta or plant remains of these when abundant—as they are here—may increase the acidity

of the substratum. For example, the peat taken from the roots of one *Osmunda regalis* registered pH 4.5. Directly below the plant, to a depth of three feet, the reactions ran: pH 5 at six inches, 5.5 at one foot, 6 at 1½ feet, 6 at 2 feet, 6 at 2½ feet, and 6 at 3 feet. Three feet away corresponding levels showed pH 6 (six inches), 5.5, 6, 6, 6 and 6. Similar tests on two plants of *Osmunda cinnamomea* in another locality gave reactions of pH 5.5, 6.5 and 6.5 for one-foot intervals in each case. Halfway between the two plants, three feet, the corresponding reactions were pH 6.5, 6.5, and 6.5.

Baroda Bog

Evidence of underlying sphagnum peat is lacking or fragmentary in the Baroda bog. Development of sphagnum can never have been more than spasmodic or very local, nor ever abundant enough to alter, except very locally, the original hydrogen ion concentration. One very small patch of sphagnum was found and traced down to an old rotten log about eight inches below the surface, where the moss started long ago but beyond which it never spread appreciably. The unwary would call this colony a relict of an ancient and a once more dominant sphagnum association. Actually it is a relatively recent and local colony.

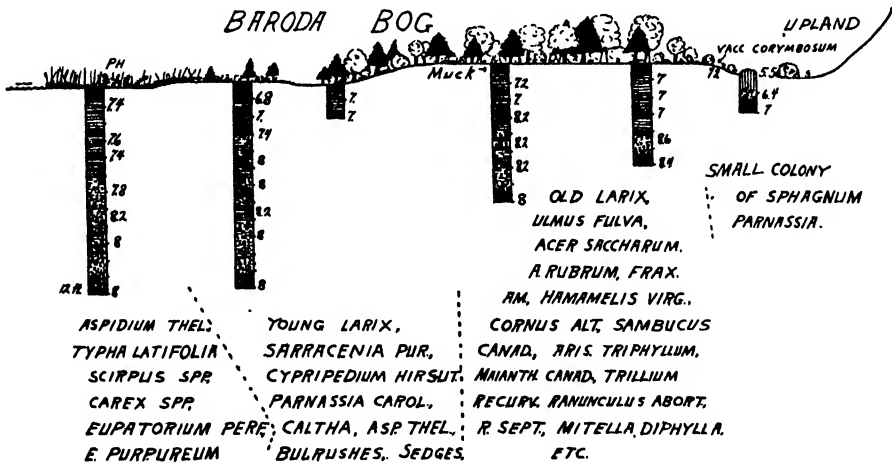


FIG. 5. Baroda Bog.

In commenting on the circumneutral reactions of the Chesterton, Cowles and Baroda bogs in the previous work ('23, p. 24) already cited, the writer states he does not know how acid, if ever, these bogs have been. The present work shows that sphagnum was never dominant nor generally distributed. Excepting the forest zone of Cowles bog with its ferns, these bogs must always have been circumneutral.

Wauconda Bog

Significance of Sphagnum Colonies.—Figure 6 shows a profile of the eastern half of the Wauconda bog. Several patches of sphagnum a foot or two in diameter were found. The absence of sphagnum directly below to a depth of 12 feet and in the samples of peat nearby, prove that these isolated and scraggly patches are relatively recent or sporadic intruders rather than "relicts." The western half of the bog is marked by more numerous and larger sphagnum colonies. Sometimes the sphagnum remains were found down to 6 feet; again not even immediately below. The writer found no extensive nor predominatingly sphagnum peat layers. Waterman ('26, pp. 260–61, 271) considers Wauconda bog a sphagnum bog of "extreme maturity" with a "few bog relicts . . . especially the pitcher plant, buckbeam, and scattered patches of sphagnum." *Sarracenia purpurea* and *Menyanthes trifoliata* are not restricted to sphagnum bogs as defined by Rigg ('25), or Waterman himself ('26, p. 255). These two plants do not therefore necessarily hark back to old, nor indicate present sphagnum bog conditions. That the sphagnum is sporadic has been shown. The evidence indicates that this bog, like the other circumneutral bogs of this paper, despite its stronger sphagnum bog tendencies, has never gone beyond the fen-moor transition (see Discussion). It is not and never has been a sphagnum bog like Sayer, Hartford or Merrillville.

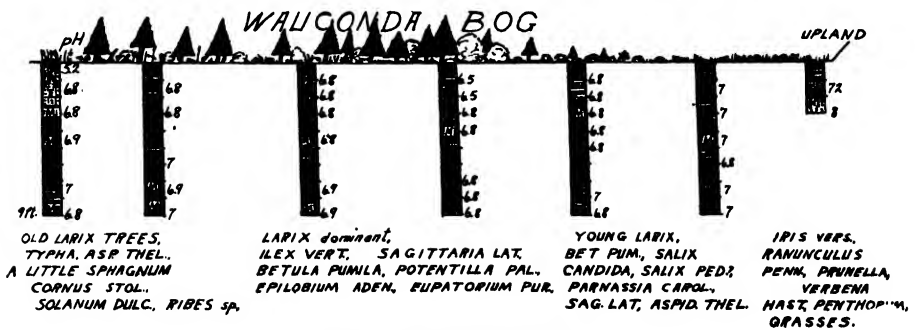


FIG. 6. Wauconda Bog.

The pH of mosses.—The influence of mosses on acidity was also studied with results similar to those found at Cedar Lake. The living tops and peat of *Leucobryum glaucum* (L.) Schimp. both registered pH 4.2, while the muck a foot below gave an alkaline reaction of pH 7.6. *Aulacomnium palustre* Schwaegr. peat showed pH 4.6; 6 inches below in muck the reaction was pH 7.6; and 6 inches away laterally pH 6.6. *Thuidium delicatulum* (L.) Mitt. living tops and peat both reacted pH 4.8, while 3 inches below the reaction was pH 6.2 and 6 inches below pH 7.2. *Sphagnum* sp. in one place showed pH 3.8, 4 inches below pH 6.8. It follows that mosses cause much of the local

acidity. Not all mosses, however, have acidifying properties. *Drepanocladus aduncus gracilescens* (Schimp.) Warnst. for example tested only pH 7.0.

County Line Tamarack Forest

The circumneutrality and abundance of shells of the County Line Tamarack Forest is pointed out by Waterman ('26, p. 267). He considers these shells exceptional. Reference to the Cowles and Baroda profiles, and to Dachnowski's ('26) recent work on New England peat deposits, however,

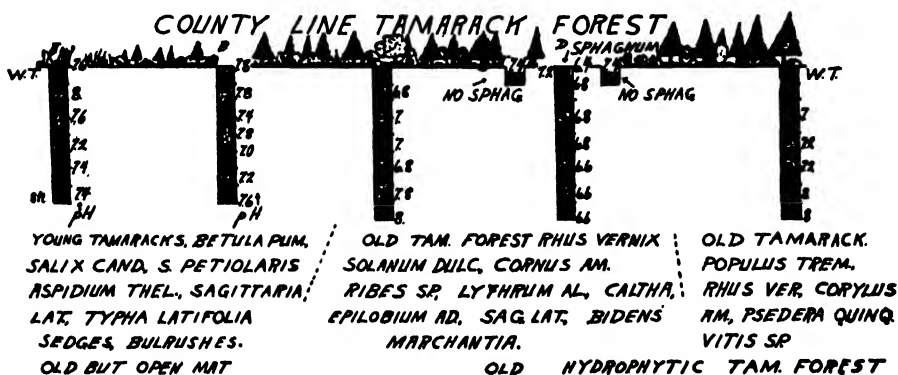


FIG. 7. County Line Tamarack Forest.

will show that marls are not uncommon in bogs. The writer found one colony of sphagnum about two feet in diameter. In general sphagnum remains are conspicuous by their absence in the substratum. This bog has never been a sphagnum bog. The statement by Waterman ('26) "Old sphagnum bogs slowly dying out in an unfavorable environment" applied to this bog is therefore untenable.

ACIDIFICATION BY MOSSES

According to Tansley ('11, p. 235) and Skene ('15), which see for citations, Paul has shown the secretion of acids by sphagnum as early as 1908. Skene found that besides sphagnum even certain mosses, lichens, leaves and other organs of higher plants exhibit acid properties. Following the method of Skene, but expressing the results in terms of pH, the writer found with him that a number of mosses "step down" the original pH of a given copper chloride solution. Although preliminary in nature the results are nevertheless indicative. A table follows:

Skene ('15) holds that adsorption of basic ions by the tissues plays a part in such produced acidity. Whatever the chemistry, we have here at least a partial explanation of bog acidity.

TABLE I. *Change produced in pH of copper chloride solution by moss*

	pH of untreated copper chloride solution	pH of copper chlor- ide solution treated with washed moss	pH of moss in field
<i>Sphagnum</i> sp.	4.4	3.0	3.8
<i>Aulacomnium palustre</i> Schwaegr.	4.4	3.0	4.4
<i>Thuidium delicatulum</i> (L.) Mitt.	4.8	3.4	4.9
<i>Leucobryum glaucum</i> (L.) Schimp.	4.8	3.8	4.2
<i>Stereodon pratensis</i> (Koch.) Lindb.	4.8	4.0	4.6
<i>Drepanocladus aduncus gracilescens</i> (Schimp.) Warnst.	4.8	4.8	7.0
<i>Calliergon cuspidatum</i> (L.) Lindb.	4.8	4.8	7.5

DISCUSSION

Bog Terms.—It is not the main purpose of this paper to discuss in detail the various definitions of bogs, moors and fens as used in America and abroad. The term "bog," when unmodified, for the sake of American custom, is applied in a general sense to both types of habitats herein studied. For the same reason the term "sphagnum bog" has been used to refer to any bog with a pronounced sphagnum-heath association. The term "acid bog" is used in a more general sense and corresponds with the moors spoken of by Tansley ('11). The habitats classified as "circumneutral bogs" on the other hand correspond with Tansley's fens or "transition moors" ("Uebergangsmoore" quoted by Tansley from Weber). On page 211 we read: "Fen possesses a peat or peaty soil fed by water, always telluric water relatively rich in mineral salts, and the ground water is *alkaline in reaction*."

On the other hand: "Moor, then possesses a relatively wet peat soil of considerable depth, fed by water, often aerial water, poor in mineral salts, so that the acids characteristic of the humous substances produced in the process of peat formation are not neutralized by bases, and the soil water is consequently *acid in reaction*."

The phrase "often aerial water" makes his definition of a moor flexible enough to fit the acid bogs of this paper. This liberal interpretation of the definition is further justified by the statement: "Under appropriate conditions, however, the fen-formation passes over into the moor-formation, by the gradual growth of plants above the reach of the alkaline ground accumulation of peat poorer in mineral salts, so that moor plants begin to supplant fen plants." This quotation is particularly applicable, for all of the bogs of this paper can be considered as fens with moor potentialities. Accordingly such bogs as Cowles, Baroda, Wauconda and County Line Tamarack Forest, in passing from fen to moor have come to a "fen-moor balance," never attaining a well-defined moor stage. Sayer, Hartford and Merrillville bogs on the other hand are full fledged moors of fen origin. Cedar Lake may be a young sphagnum bog as both Emerson and Waterman hold. If so, it would be a moor also. But satisfactory disposition of its status is impossible with-

out data on the abundance of sphagnum remains in the lower horizons. Whether Duck Lake bog more nearly approximates a fen or a fen-moor balance depends on where the line distinguishing the one from the other is to be drawn. It must be understood that the very dynamics and intergradations of bogs will sometimes make rigid classifications impossible or useless.

Rigg ('25) defines a "sphagnum bog as that stage in the physiographic succession of an area during which its surface is entirely devoid of ordinary 'hard' soil and is composed entirely of living or entirely or partially disintegrated sphagnum, the habitat exercising a distinctly selective influence on its flora." The acid condition caused by the very presence of sphagnum ought, however, to be understood in such a definition. Waterman ('26) also lays down a definition of a bog. On page 255 we read: "A bog is characterized in general by a xerophytic vegetation containing such specialized forms as pitcher plant, sundew, cranberry and sphagnum, accompanied by an acid substratum.

"In a swamp on the other hand, characteristic bog plants are absent and the substratum is alkaline or neutral."

These concepts are not very satisfactory. For, the terms "bog" and "swamp" have been used in a general and interchangeable sense too long. Even Waterman himself ('26, p. 265), speaks of "Sphagnum-Sarracenia bogs" in Florida. These habitats in Florida flatwoods with scant peat development and solid substratum, their similarity in physiognomy notwithstanding, present a striking contrast to bogs of the north. Likewise his definition of a swamp does not apply to the acid cypress, gum or juniper (*Chamaecyparis thuyoides*) swamps of the south. Somehow Waterman has not applied his own definition consistently. Although he, as well as the writer, found Wauconda bog and County Line Tamarack Forest to be circumneutral in reaction; and although he states acidity as one condition of a bog, he nevertheless lumps these two habitats in with his nine sphagnum bogs.

Other Classifications of Circumneutral Bogs.—Previous workers have in effect also recognized circumneutral bogs and have classified them variously. For instance, Cowles ('01) describes an "undrained swamp (peat bog) at Dune Park," Indiana, which seemingly resembles those of this paper in its flora but is said to have a hard sandy soil. Davis ('06, p. 212) makes a list of nine kinds of bogs, swamps or marshes for Michigan. His "Tamarack swamps, marshes and bogs," and "Grass and sedge marshes and bogs" are non-sphagnous bogs. Pennington ('06), also working in Michigan, says: "Peat bogs are heterogeneous habitats and require detailed study." Transeau ('06), in his Michigan study says: "Where the habitat dates back to Pleistocene times and has remained undisturbed we find today the bog flora. Where the habitat is of recent origin or has been recently disturbed, we find the swamp flora or a mixture of swamp and bog species." In northern Iowa too, Pammel ('09) found "marsh and sedge bogs" with no trace of sphag-

num. Dachnowski ('26) too gives some peat profiles of New England which include deposits without sphagnum. Some he calls "cedar swamps" or "swamps." His "swamps," as well as the other variously classified habitats gone over in this paragraph, seem to resemble closely the circumneutral bogs of this paper or the fens and transition moors of Tansley.

Acidification of Bogs.—The acidity of sphagnum bogs is common knowledge—see Dachnowski ('12), Livingston ('05), Transeau ('06), Warming ('09) and others. And, the acid properties of sphagnum and other mosses has been discussed above. But there is need of more data showing the part played by sphagnum and other plants in influencing hydrogen ion concentrations. Chodat ('24) for one, points out that sphagnum increases the acidity of the substratum. Christopherson ('25) suspects sphagnum of lowering the pH of the substratum. Waterman ('26) writes: "The observations already given in detail, show that in these Illinois bogs, where bog plants are present the substratum is always acid, and conversely, where no bog plants are found the substratum is neutral or alkaline." But he does not point out any correlation between any particular bog plants and acidity. Or, on page 267 we read: "The question then arises as to the time at which acidity will appear in the mat . . . it would seem as if normal acidity of a bog is developed only after the growth of a considerable mass of filling plants with their underlying peat . . . and the factor most influential in permitting or preventing this development of acidity would seem to be the activity of the wind." According to this hypothesis, wind is supposed to "prevent the formation of the initial framework of sedges and grass" (fillers). Also in shallow places water is supposed to be neutralized by calcareous sediment of uplands, while the reserve acidity of the deeper water would make conditions more favorable for the formation of an acid mat—if the writer interprets Waterman correctly. This explanation may be countered in at least two ways: First, even the deeper waters of Cedar Lake with its incipient sphagnum bog are highly alkaline. Emerson ('21) found the water to be "uniformly 30 alkaline" (pH 8.5). Waterman himself states that the free water of this lake is alkaline. So, here we have a lake which despite its alkaline free waters and circumneutral mat, supports locally acid sphagnum and moss colonies. Secondly, in this explanation Waterman does not single out sphagnum itself as an important acidifier. The data of the previous pages corroborate Chodat's conclusions, Christopherson's suspicions, and the writer's own former observations ('23, p. 23), and show quantitatively the rôle sphagnum plays in building up acidity of bogs. However, it should be remembered that other plants, like the Osmundas or certain mosses, as already shown, may play a similar though less pronounced part.

Establishment of sphagnum.—The relation between the initial reaction of the free water and of the mat to the establishment of sphagnum is still moot and needs more data. One notices that the two most typical sphagnum

bogs—Hartford and Sayer—show a slight acid reaction of pH 6–6.5 even in the non-sphagnous frontier. Of course the free and deep waters run definitely alkaline. Cedar Lake, on the other hand, where sphagnum is well established in places, runs to definite alkalinity in the non-sphagnous places immediately around and below the sphagnum. It will also be seen that typically non-sphagnous bogs are on the whole entirely circumneutral or markedly alkaline. In the laboratory Olsen ('23) found that, in general, growth of sphagnum took place in cultures with reactions running from pH 3.5–5.5 depending on the species. *Sphagnum subsecundum* grew slightly even at pH 6.5. Just what such a sphagnum would do in nature where the acidity would be cumulative once the plant established itself, is another matter. Skene ('15) demonstrated that in general sphagnums hold a "repugnance" for alkalis; at the same time he points out that certain species can tolerate a slight concentration of hydroxyl ions. In fact, Mr. J. C. Isenborger, working in the Hull Botanical Laboratory at the University of Chicago, germinated without difficulty *Sphagnum acutifolium* Ehrh., here the commonest acid bog species, in a marl solution of pH 8.4. At the writing of this paper the young thalli look vigorous. However, in the absence of more data from the laboratory and nature along these lines, definite conclusions must be held in abeyance. This much is safe to say: a very slight acidity, if at all necessary, other factors being favorable, will suffice to initiate and establish sphagnum; then, once established, it will per se increase the acidity.

Influence of Sphagnum on Reactions of Lower Strata.—Christopherson ('25) found that the high acidity of bogs of Sylene National Park, Norway, prevailed to a maximum depth of 64 cm. He attributes this to the downward movement of strongly acid water from the upper horizons. But according to his peat analyses he seems not to have penetrated down beyond sphagnum remains. The old underlying sphagnum remains, if present in quantity, might easily account for the high acidity of his lower strata, so enduring is sphagnum acidity. For example, the Hartford Sphagnum bog is old enough from a successional standpoint to support a deciduous sub-climax forest in the oldest zone. Yet we find well preserved and packed sphagnum only a foot below the surface, with a reaction of pH 3.4. However, the sphagnum bogs of this paper show a sharp decline in acidity immediately below and laterally away from sphagnum, especially where alkaline waters from below bathe the peat.

SUMMARY

In this paper the term "bog" has been used in a general sense to include both acid and circumneutral bogs. The acid bogs correspond with the moors of Tansley. In such a scheme, Rigg's sphagnum bogs would be particular kinds of acid bogs or acid moors. The term "circumneutral bog," more inclusive, may take in fens at one extreme and fen-moors (transition moors of Tansley) at the other. Many of our so-called "swamps," "tamarack

swamps," "tamarack bogs," "cedar bogs," "cedar swamps," "mixed bogs" and so on, fall under the general category of circumneutral bogs, and specifically into either fens or fen-moors. In conformity with common practice the writer regards peat as part and parcel of bogs. However, the data show that bogs in the general sense, contrary to some opinions, are not necessarily or even usually acid; and that acidity is not prerequisite for peat preservation. Further, the very establishment and dominance of sphagnum and certain mosses and even other plants results in high acidity and the interpolation of an acid-heath stage in bog successions. Conversely, failure of such species to become established or dominant permits some bogs to remain circumneutral throughout all stages of succession from fen to forest.

Incidentally, the plant lists accompanying the profiles show that a good number of bog species tolerate a wide range of reaction.

The writer owes much to the conferences held with Dr. H. C. Cowles of the University of Chicago and to Dr. Geo. B. Kaiser of Pelham, Philadelphia, for his determinations of the mosses. Thanks are also due to Messrs. S. S. Shearer, J. P. Lusk and E. P. Slone for their field assistance, and to the Hull Botanical Laboratory of the University of Chicago for the use of reagents and equipment.

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NOTES ON THE LIFE HISTORY AND HABITS OF THE MOUND-BUILDING ANT, *FORMICA ULKEI* EMERY¹

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INTRODUCTION

In two sections of the Cook County forest preserve near Chicago, there occur two very large groups of colonies of the ant, *Formica ulkei* Emery.² These colonies are located at Palatine and Palos Park, Illinois. The enormous mounds which these ants build attract the attention of anyone passing through these woods. Yet, curiously enough, very little has been known about the life history and habits of this species, and nothing at all about its hibernation, a life history phase of special interest to the writer. The enormous number of individuals in each nest, the availability throughout the year, the ease with which the ants could be maintained in the laboratory, made them very favorable material for study. Accordingly, observations were begun on their life history, concentrating especially on the hibernation phases. The notes on the life history and habits are herewith presented, while the hibernation studies will be included in another paper.

GENERAL METHODS OF STUDY

The study of these ants was begun in the fall of 1924. Throughout the fall, winter, and spring of 1924-25, the nests at Palatine were visited every ten days. The prime purpose of these regular field trips was to obtain information on the over-wintering phenomena. The nests were penetrated usually to soil water level. Specimens of ants and other inhabitants of the nests were collected for examination and identification, and for various physiological experiments; the character of the nests was noted and such life history and habit data collected as came to light. In addition to these trips, a number of trips were taken at irregular intervals in the summer of 1926 to both the Palatine and the Palos Park colonies in order to gather further life history data and to study their habits during the active season of the year.

Several artificial nests were established in the laboratory. These nests furnished most of the data on egg laying and rearing, and some of the observations on the habits of the ant. For maintaining ants in large numbers, a pan was constructed of galvanized tin about 12 inches square and about

¹ This work was done at the University of Chicago. I am indebted to Dr. W. C. Allee for his aid and interest.

² Identification by Dr. W. M. Wheeler. The description of the species may be found in Wheeler, 1913, pp. 481-484.

2½ inches deep. In the center was a water-tight, walled-in area, 6 inches square, in which soil and ants were placed. Around this was a water moat about 3 inches wide to prevent the escape of the ants. It was soon found advisable to hang strips of tin bent in appropriate fashion on the edge of the ant chamber or nest proper on all four sides. These strips provided convenient return paths for the ants which fell over the edge of the chamber in their excited activity when disturbed, and so prevented an appreciable loss by drowning. The ant chamber was covered by a loose, opaque cover so that evaporation from the soil might be reduced to the minimum. These nests were well suited for stock nests, but were poorly adapted for close observational work because of their depth and because the soil necessary in the nests interfered with the vision.

The nests devised by Miss Fielde (Wheeler, '26, pp. 551-554) were tried out for smaller groups of ants requiring more detailed observation. These nests are made of two glass plates supported by glass strips glued around the border of the bottom plate, so that the ants are at all times visible. Such nests are, however, inconvenient when one wishes to feed the ants, clean or otherwise enter the nest, since the much too lively ants often escape before the covering glass plate can be replaced. This type of nest was not used extensively.

The most convenient method for close observation of small groups of ants proved to be the finger bowl nest. This consisted of a finger bowl with moist blotting paper covering the bottom, and another folded piece of moist

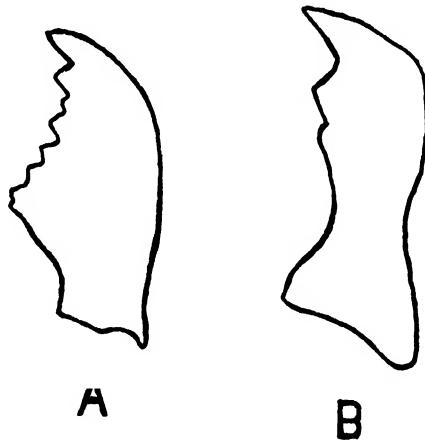


FIG. 1. A. Right mandible of female, showing the typical 8-toothed arrangement. B. Right mandible of male, showing 3 teeth present.

blotting paper under which the ants could crawl; a glass plate covering the finger bowl prevented the escape of the inhabitants. To feed the ants or to clean the nest, it was only necessary to set the finger bowl in a shallow basin of water before removing the glass plate.

All the laboratory ants were fed various types of food, but the ones that proved most attractive were apple, banana, honey and other insects. All the nests were kept at room temperature.

The description of the species given by Wheeler ('13) need not be repeated, but attention is called to the mandibles of the male which have been described as edentate, but in all those examined three teeth were present as shown in figure 1. Plate VI shows the relative size and proportions of the various castes occurring in this species.

ECOLOGY

Formica ulkei has been reported from Wisconsin, South Dakota, Illinois, Nova Scotia and New Brunswick. "This species is evidently peculiar to the Canadian fauna and so rare in the transition zone that I have never had the good fortune to find one of its colonies," writes Wheeler ('13, p. 487). In Illinois, it has previously been reported only from the Chicago region. And here it occurs only in the two places already mentioned, Palatine and Palos Park. These two habitats are about forty miles apart, but are so similar that they can be described as one.

The forest in which the ants occur is of the oak-elm-hickory type, still in a natural state though not virgin forest, occurring on a series of low hills with low, ponded areas scattered through the woods. Some parts of the forest are rather dense with underbrush and high weeds; other parts are more open. The ant nests are in the more open places, some along the edges of the low areas, others on the higher ground. Plate VII, Fig. 1 shows a portion of the woods adjoining a low spot. Five mounds may be seen at the edge of the woods. There seems to be a careful avoidance of the deeper, shaded parts of the forest, so that all nests are exposed to the sun at least a part of the day. No nests occur in the fields and pastures adjoining the ant-inhabited sections of the woods. The confinement of the nest locations to the woods is very striking. A small section of the woods, less than an acre in extent, was found separated from the main body by a strip of low meadow only about thirty yards wide. Although there were a number of nests in the main body, only two colonies had established themselves in the small isolated woods. Even this small strip of open meadow acted as a partial barrier. Only one instance of a nest outside of the woods came to my attention. It was located across the road from the forest edge along the fence surrounding a meadow, but was completely surrounded by high weeds and a small amount of shrubbery. All these facts indicate that this species is limited to the open forest and the forest margin.

The forest floor is covered with decaying leaves, grass and weeds. The soil is black, rich loam underlain with a layer of yellow clay several feet deep. The surface soil is acid. The soil water level fluctuates with the season, but is always near the surface, from a foot to five or six feet in depth, depending

on whether the nests are located on high or low ground. Because of this close proximity of the soil water to the surface, the nest is kept rather moist throughout the year, though in dry seasons the mound may become dry and hard.

THE NEST

Formica ulkei, like *F. exsectoides* of the eastern states, which it resembles in appearance and habits, builds a prominent mound out of the excavated soil and debris of the nest. (See Plate VII.). These mounds vary greatly in size. The youngest nests observed are about one foot in diameter, while the older, more heavily populated ones may have a mound several feet in diameter (the largest seen was nine feet long, seven feet wide and two feet high). Usually, the mounds are circular, but the largest are nearly always elongated. The apex may be pointed or rounded. The mound of the smaller, younger nests is usually covered with grass, but this is seldom the case with the larger, well-populated nests. Numerous holes occur on the surface of the mound, not in the form of craters, but mere openings in the surface.

A large number of nests have been entered and the inner architecture noted. The material composing the mound is largely excavated soil (mixed loam and clay). On the surface is a thin layer of mixed soil, grass, roots, small twigs, buds and other debris, about an inch thick, and frequently very dry, forming a crust (see Plate VII, Figs. 2 and 3). This crust is also much undermined, and the wide, low spaces underneath it parallel with the surface permit one to raise it up in thin chunks. Below the crust, the mound is much burrowed out with many connecting galleries running parallel to the surface, some vertically, and here and there small cavities for the storage of the young. The burrows penetrate deeply into the ground, extending down to soil water level in every nest opened, whether located on high or low ground. Since the ants spend most of their active life in the upper parts of the nest, it was found that the burrows were most numerous in this portion. They do not appear to extend beyond the border of the mound. However, the finding of a single specimen of *Cyclops*, and two of *Gammarus*, in the soil water of one of the nests about 25 feet from the pond indicate some sort of a connection between the nest and the pond. It would be difficult to conceive of these crustaceans gaining access to the water in the nest by simple seepage through the soil; they are too large for that. And there was no chance of accidental contamination. No galleries were found extending between the various nests, as is the case with some species, but I am not ready to state positively that none exist.

Nests located on high and low ground were opened for purposes of comparing their architecture. No essential difference was found, except that the burrows extended deeper into the ground before soil water was reached in the case of the high ground nests, whereas the burrows were necessarily limited in depth in those located along the border of the low areas.

LIFE HISTORY

Toward the close of the hibernation period (April), field trips were made to the ant colonies, and a large number of hibernating specimens collected for observation in the laboratory. These comprised several wingless females and a large number of workers, the only stages which hibernate. The ants were temporarily kept in artificial nests in cold storage until activity began in the nests in the field. Seven small colonies were then established in the laboratory (April 21, 1926) in the finger bowl nests already described, and two (No. 6 and 7) on May 10 in Fielde nests. Each colony contained a single female and five or ten workers to care for her. All nests were kept at room temperature. The colonies were observed continuously until all but one of the females were dead. Record was kept of each batch of eggs. A few life history notes were obtained from large stock nests, some of which were established in April, 1926, and others in the fall of 1924. These notes were from chance observations, but are introduced in support of other observations made in the laboratory. The laboratory notes have been checked up with those obtained in the field so far as possible.

A large number of eggs was obtained from the females; but a large mortality occurred in the young due to the cannibalistic tendencies of the workers. Eggs and larvae disappeared continually. Cannibalism is common among ants, and constitutes a difficulty in the rearing of the young in laboratory nests. Tanquary ('13) and Reichenbach ('02) also reported this difficulty in the rearing of *Lasius niger*. Some of the *F. ulkei* eggs failed to hatch for other reasons. As a result, only 9.7 per cent of the 903 eggs for which complete records are available produced larvae (see Table II). Of these larvae, only 1 attained the pupal stage.

A number of eggs was obtained from workers. No mature females of the usual type were present in the nests in which these eggs were found, since they were wanted for rearing experiments, and were carefully picked out from the rest of the ants, and placed in separate rearing nests. It is possible that the eggs may have been laid by worker-like females, but polymorphism has not been studied in this species. The laying of eggs by workers is commonly reported in the literature on ants.

An interesting point should be recorded here. Females appeared in the larger nests which had been stocked only with workers. That these females were not accidentally overlooked when the nests were established is attested by the finding of large, empty, pupal cases in the water moats of these nests. The old controversy as to the application of the Dzierzon theory of sex determination to ants will hardly be settled by the above observations, since the virginity of these workers is doubtful. Seminal receptacles have been found in some of the workers of other species,* so it is possible that workers may be fertilized by males. Males have been seen to pursue workers with as much

* Work of Miss Holliday, reported by Fielde ('05).

energy as they do females (Fielde '05), though copulation of males with workers has never been observed (Wheeler '26). Fielde obtained only males from the eggs of virgin females and workers in four species of ants, and concluded that unfertilized eggs of ants produced only males. Further observations and more carefully controlled experiments would be needed to determine this point for *F. ulkei*.

In the data given on the rearing experiments, only such as are free from these and other disturbances have been used.

The first active female was found among active workers close to the surface of the mound on April 11, 1925. On May 2, all the females were found in the upper burrows, none being found at the bottom of the nest in the aggregations of workers which were still hibernating.

The first batch of eggs was found in the laboratory on April 27, six days after the establishment of the nests. The other females of the laboratory nests began laying during the first few days of May. Most of the egg laying took place in the latter part of April and early May, but some females continued laying even up to the first days of June. No eggs were obtained thereafter (see Table 1.). Eggs were first found in the field on May 2, 1925;

TABLE I. *Dates of egg laying for F. ulkei in the laboratory*

Serial No. of female.	Date of first laying.	Date of last laying.	Total eggs laid.	Remarks.
1	Apr. 27	May 24	182	These eggs were not removed. These eggs not removed.
2	Apr. 26	June 7	167	
3	May 3	June 2	147	
4	May 3	June 17	190	
5	May 1	May 19	126	
6	May 17	May 19	About 50	
7	May 19	Only 1 mass laid.	About 50	
8	May 3	May 10	126	
9	May 3	June 17	128	

this date coincides well with the appearance of eggs in the laboratory nests of 1926. These eggs were found both in the surface soil of the mound and in the wet clay at the bottom of the nest where the ants hibernate. The latter may either have been laid there, or carried there subsequent to laying in an apparently erratic manner by workers. With the exception of the two batches of eggs referred to as having been found at the bottom, all eggs were near the surface, and it seems safe to assume that this is where they are laid. Very young larvae were found on the field trip of June 18, 1925, but no eggs. On June 26, 1925, no eggs were found, and the larvae appeared to be much larger. It is evident that egg laying had ceased some time before the middle of June. It seems, therefore, that the normal egg laying period extends from the latter part of April to the early part of June. The date will vary somewhat from one season to the next. Nests kept in the laboratory at room

temperature all winter showed eggs and even larvae in January, 1925. This hastening of the egg laying period is a well known phenomenon due to the warm temperature at which the ants were kept.

Each batch of eggs was removed as soon as laid in seven of the finger bowl nests, and placed in a separate finger bowl together with 5-10 workers to care for the eggs; a record was made of the date of laying and of the subsequent history. Each of these seven females laid a large number of eggs, the maximum being 190 +, and the minimum 126 for each female (see Table I). The eggs were laid in batches of 1-51 eggs with an average of 13.8 per batch. The laying of a representative female (No. 1) is given below:

Apr. 27.....	36 eggs	May 10.....	16 eggs
Apr. 29.....	10 "	May 11.....	6 "
Apr. 30.....	13 "	May 13.....	4 "
May 3.....	12 "	May 17.....	14 "
May 5.....	19 "	May 19.....	12 "
May 6.....	4 "	May 20.....	4 "
May 7.....	20 "	May 24.....	8 "
May 8.....	4 "		
		Total	182 "

In the above record and the record of other females, the egg laying proceeded in rhythms, the laying of a large batch of eggs alternating with the laying of a series of smaller batches, the high peaks in these rhythms occurring just a few days apart.

In the other two laboratory nests (No. 6 and 7), the eggs were not removed. These females had been collected at the same time as the other seven (April 12), but had been kept in cold storage until May 10 when they were placed in Fielde nests together with a few workers. Female No. 6 began laying on May 17, and by May 19 a mass of about 50 eggs had been laid. This female laid no more. Female No. 7 laid one large mass of about 50 eggs and none thereafter. The difference in treatment of these two females as compared with that of the other seven may account for this difference in egg laying.

The eggs hatch into the usual legless, white larvae, shaped very much like a summer squash (see Plate I). The time of hatching for *F. ulkei* appears to be somewhat variable (9-16 days), but the average is about 12 days (see Table II). This is shorter than that recorded for *Aphaenogaster fulva* (17-22 days, usually 19 days, Wheeler, '26, p. 81), of *Myrmica rubra* (23-24 days, Wheeler, '26, p. 81), or of *Camponotus herculeanus pennsylvanicus* (24 days, Pricer, '08).

The length of larval life in *F. ulkei* is uncertain. For the only pupa obtained in the rearing experiments in the laboratory the larval life was 21 days. In *Aphaenogaster fulva*, the larval period is reported as 24-27 days, that of *Myrmica rubra* 30-71 days, and of *Camponotus herculeanus pennsyl-*

vanicus 21 days. The larval period is very variable in most ants, depending upon the quantity of food which is given the larvae. Tanquary ('13) reported that he maintained larvae of *Lasius niger* in a nest for over a year, and other observers have obtained similar results. Larvae were present in the field nests of *F. ulkei* until August 16 (1926), at which time only large ones were found. On September 1 (1924) no larvae were discovered.

TABLE II. *The number of larvae hatching, and hatching time, for eggs of F. ulkei*

Serial no. of female.	Total no. eggs laid.	No. larvae hatched.	% of eggs hatched.	Variation in hatching time.	Av. time for hatching.
1	182	21	11.5	11-14 days	12 days
2	163	11	6.7	12-14	13
3	131	11	8.4	9-15	12
4	158	20	12.6	11-14	12.5
5	126	1	0.8	13	13
8	26	18	69.2	11-16	12
9	117	6	5.1	10-16	13
	903	88	9.7 av.		12.5 av.

No data were obtained on the pupal period in the laboratory. The first indication of worker pupae in the field was on June 18 (1925), when several pupae and larvae were found. These pupae continued in the nests in the field for a short time after the onset of hibernation.

Although eggs, larvae and worker pupae had appeared in the field nests by the end of the 1924-25 season's collecting (June 26), no indication of the young of the larger, mature, sexual forms had been seen. On July 8, 1926, the first field trip that summer, a few very large pupae were taken from among the smaller worker pupae; these were reared and proved to be the pupae of mature males and females.

On the next field trip (July 14, 1926), large male and female pupae were numerous, and found near the surface of the mound. A number of recently-emerged, winged males and females and a number of active, winged males were also found, besides a larger number of worker pupae and a smaller number of larvae. No callows were seen on this date. This seems to be the approximate date of emergence of the mature sexual forms in the field. It seemed from the condition of affairs in the nest at this time that the nuptial flight, if one occurs, must be near. I was unable to remain with the ants continuously to see their mating activities.

On July 20, another trip was taken. At this time, I dug over the entire mound to a depth of one foot, and made a special but unsuccessful effort to find the large pupae; so all sexually mature forms must have emerged by this time. Several dead males were seen, and a few, live, active males, some of which dashed out of holes in the mound. The females were still winged, and crawled out very actively on the surface of the nest, on twigs and other nearby

objects. A large number of workers crawled up and down the trunk of a large tree bordering the mound. Such behavior I had not before seen in this species. The picture presented was such as one might expect to see at or just after the mating season—some dead males, males and females still winged and active outside of the nest. I was led to conclude that mating was just taking place, or had just occurred, though I did not actually see the mating activities.

Three days later at Palos Park, no male or female pupae were found, but mature, winged males and females were present. There was no apparent inclination for the males and females to crawl in the open on the surface as on the last field trip. Several sexually mature individuals were collected in separate vials to see if they could be mated in the laboratory, but without success.

While I was not so fortunate as to see the mating of *F. ulkei*, the facts seem to warrant the conclusion that this life history phase took place on or about July 20, 1926. I am also inclined to believe that the nuptial flight is very limited in extent judging by the limited distribution of the species.

Several attempts were made to observe the deälation of the females in the laboratory, but without success. However, two deälated females were found in a large stock nest in the greenhouse on August 4, 1926; these were young ones that had emerged during the summer.

Callows were seen in very small numbers in the field on July 23, 1926, when worker pupae were very numerous, and only larger larvae were found. This date seemed to represent the beginning of the period of emergence from the pupal cases. Larvae were diminishing in numbers until August 16, 1926, when only a few large ones were present. On September 1 (1924), only workers, worker pupae and callows were found, but no larval forms were taken on or after this date. The pupae were still in the upper six inches of the mound soil. On September 10 (1924), the pupae were in small groups of 2-3 at the bottom of the nest about six inches above the soil water level. They were still numerous, however. At this time, also, many of the workers were found in small, loose aggregations just above the soil water level, where they were entering hibernation. Others were still active on the surface of the mound. A few days later, the pupae were fewer and the aggregations of hibernating workers greatly augmented. By October 21 (1924), all the pupae had disappeared from the nests. And by November 1 (1924), the callows were indistinguishable from the older workers. This was also the last date on which surface activity was noted, and all the colonies were definitely in hibernation.

The winter is spent in the deeper burrows of the nest just above the soil water level. The ants (workers and mature, deälated females) aggregate in very dense masses numbering thousands of individuals in the wet clay at this level. A few scattered individuals may be found in the upper frozen

soil often surrounded by frost crystals. These are no doubt the ones that were tardy in seeking winter quarters and were caught when the first cold weather chilled them. They are also the ones which first resume activity in spring when the frost leaves the ground. There is some evidence for thinking that they are responsible for the general awakening of the whole colony in the spring, when the surface earth becomes warmed. Activity begins again in the spring simultaneously on all the nests just as soon as the frost is out of the ground.

The ants maintain a very sluggish state of activity throughout the winter. They are able to crawl slowly to cover when disturbed, and quickly become active when warmed. In this respect, they are different from some Hymenoptera (e.g., *Vespa*, *Camponotus*, etc.) of this region, which can scarcely be roused from activity by ordinary warming methods. Further details on the hibernation phase of the life history of *Formica ulkei* will be given elsewhere.

FOOD AND FEEDING HABITS

The food of *Formica ulkei* is varied. Different foods were tried out in the laboratory nests. The ants are quickly attracted to sweet fluids which they lap up voraciously. Sugar solution, syrup, and honey proved successful; the ants seem to be especially attracted to honey, no doubt, because of its strong odor. Fruits were also introduced; apple and banana were greedily devoured. Here, too, the smell of these fruits seemed to attract them. Occasionally, fresh insect bodies were cut up into bits which the ants ate. On several occasions, insect bodies have been found in the nests in the field, so other insects normally constitute part of their diet. Attention has already been called to the fact that the ants feed on their own young in the laboratory nests. It is conceivable that this happens also in nature, especially at times of food shortage. A rather large number of tree buds were found in the nests in the field, and it is probable that the ants obtain sweet materials from the surface of these buds.

Like most ants, *F. ulkei* makes use of aphids to secure the sweet honey dew which they secrete. Small groups of wooly aphids were found in the galleries of the nest on several occasions during the winter; and on August 14 (1926), workers were observed in attendance upon some black aphids (species undetermined) on a small poplar.

Males and females have both been observed to feed directly upon the food put into the nests. Females are commonly seen being fed regurgitated food by the workers, but the males were never observed receiving any attention. Workers often definitely solicit food from their fellows by the usual method of stroking the head with their antennae.

There is a keen sense of smell that leads these ants directly to the food. As soon as honey is put into the finger bowls, invariably the nearby ants wave their antennae in various directions and then start crawling in an al-

most straight line for the food. This striking behavior was seen time and again.

The very active crawling of the workers makes it possible for them to cover a considerable range in their foraging expeditions which extend out into the surrounding grasses and weeds. These expeditions are not organized, but each worker shifts for herself. Several attempts were made to determine how far they strayed from the edge of the mound. An isolated nest near a recently cut meadow gave the best opportunity. There, just after noon on a day in mid-August, a worker was found 57 feet from the nest mound. None were located at a greater distance.

CARE OF THE MEMBERS OF THE COLONY

The eggs cohere in small masses which vary up to about 50 in number. These masses are carried about by the workers, and deposited in various parts of the nest. The larvae stick together in masses by means of the hairs on their bodies, and are fed with regurgitated food by the workers. They are sorted out according to size, so that scattered masses of larvae may be found in the nest, each mass containing larvae of the same approximate size. The pupae are kept separate from the larvae. Usually, the pupae are placed rather near the surface of the mound, exposed to warmer temperatures and drier conditions. The cocoons makes them resistant to drying, and enable them to profit by the higher temperatures at the surface level of the nest. The larvae are usually found in deeper parts of the mound than the pupae. At the beginning of hibernation, those pupae still remaining are carried to the bottom of the nest near the soil water level, and there the last callows emerge. The pupae at this time of the year profit by the more constant temperatures at this level as compared with the fluctuating temperatures of the surface.

Great solicitude is shown the females. Several workers may attend a single female at one time, keeping her body immaculate and shiny, and sometimes feeding her, as before described.

The stronger workers often carry the weaker or exhausted individuals bodily to or from the nest. This may occur in migrations from one nest to another, or on foraging trips when individuals venture too far and cannot return in their exhausted condition. This form of solicitude has been observed on several occasions in the field and in the laboratory. Once a large stock nest had become accidentally flooded over night. To save the ants, a bridge was constructed from a strip of tin appropriately bent, extending from the flooded nest over the water moat to a freshly prepared nest. In order to get the ants to move into the new nest, a few workers were placed upon the bridge. These crawled to the new nest, explored it, and some returned to the old nest, where they caught up the other ants one by one in their mandibles and carried them up on the bridge and into the new nest. The

transported ants always carefully folded up their legs against their body, thereby facilitating the transportation. They looked like dead ants, while they were being carried, but as soon as they were deposited in the new nest, they began to crawl around exploring the new abode. This carrying of workers has also been observed on the surface of the mounds, and always in the manner described.

CARE OF THE NEST

Surface activity begins as soon as the frost is out of the ground, and increases in intensity gradually until all the ants are out of hibernation. They desert the lower galleries near the level of the soil water and spend all their time during the active season on or near the surface (upper 6 inches). Here, they busy themselves with the care of the young, foraging, and the almost constant repair of the nest. Workers are seen on the surface carrying the tiny sticks, blades of dead grass, small particles of soil, empty pupal cases, etc. After rains, the collapsed surface crust must be repaired, and new exits made. These are all very common sights on any ant mound.

Sunlight does not seem to hinder the ants in their surface activity. It is interesting to note that on a very warm day, however, they confine their attention to the shaded parts of the mound and along the grassy edge of the nest. This statement is based on the following observations: On July 20 (1926), the air temperature in the shade was 33.5° C. at 1:20 P.M., and the temperature of the surface soil of the mound exposed to the sun was 41.6° C. Not one of the 18-20 nests examined showed any activity on that part of the mound which was exposed to the sun, but, on the contrary, all surface activity was confined to the shaded portions of the nest. This was a reaction to the intense heat rather than to the light, for on other sunny days, surface activity was normal in the sunny as well as in the shaded portions of the mound.

Activity continues thus at or near the surface until the early days of fall when the ants gradually retire to the deeper parts of the nest and begin hibernation. Surface activity gradually diminishes; but not until the ground freezes do the ants cease their work entirely.

RELATION TO OTHER ANIMALS

Formica ulkei defends its nest against invaders or disturbers of the nest with great vigor. Any disturbance causes the workers to swarm in large numbers to the point of attack, and to dash about wildly in mad confusion. They rush at the invader with mandibles wide open ready to fasten on the attacker. When once the mandibles are fastened on an object, it is very difficult to dislodge the ant. The abdomen then bends ventrally so that the posterior tip is directed anteriorly and emits therefrom a fine jet of formic acid which enters the wound inflicted by the mandibles and may kill the

enemy. This formic acid is very powerful. Each worker may secrete a drop of it about half the size of the head of an insect pin. If the ant is confined in a closed space, such as a stoppered vial or a weighing bottle, it is quickly killed by the fumes of its own acid. It is well nigh impossible to handle the ants without stimulating them to secrete this acid. This proved to be a real difficulty in experimental work.

On one occasion, the last stages of a real battle was witnessed between *F. ulkei* and a species of small household ant (*Monomorium pharaonis*?). A large number of *F. ulkei* workers had been placed in a dish-pan covered with a fine-meshed wire screen to prevent their escape. One day, it was discovered that a large number of the tiny household ants were running up and down over well-beaten paths to and from the laboratory nest. Upon looking into the nest, I beheld a desolate scene,—my laboratory ants scattered over the surface of the nest, still alive, but with mere stumps of legs remaining, and with several of the tiny ants still clinging savagely to the remaining stumps. *F. ulkei* had been completely routed by the superior numbers of its tiny enemies.

When the first survey of the colonies of *F. ulkei* was made, it was found that there were scarcely any nests of other species of ants in the vicinity. Only two nests of *Proformica neogagates* were found. Later a nest of *Lasius (Acanthomyops) interjectus* Mayr. was found. These three nests were only 3–5 feet apart and 12–15 feet from the *F. ulkei* nests. Yet they flourished and were unmolested in the midst of the large number of *F. ulkei* colonies. This would indicate that *F. ulkei* is not an aggressive species.

Throughout the extensive excavations of the nests, collections of other species of animals have been made and a record has been kept of these collections. A list of the species taken and the dates of collection are given in Table III.

Nests have been found on all occasions to be practically free from other species of ants. A single specimen of *Myrmica scabrinodis* Nyl. was taken from a nest on April 11; and on July 26, a female of the same species was discovered in a laboratory nest, but had been entirely overlooked in the field. Presumably, it must have been obtained from the *F. ulkei* nests when the workers were collected for experimental use. On October 11, a single specimen of *Crematogaster lineolata* Say was collected from the surface of one of the weaker colonies. On June 18, a single specimen of *Lasius (Acanthomyops) interjectus* Mayr.⁴ was collected from the deeper parts of another nest. These are the only instances of the occurrence of other species of ants in or on the *F. ulkei* nests that have come under my observation. *F. ulkei* is not a slave-maker, and defends its nest with such energy that very few individuals of other species can gain access.

⁴ Since the above observations were made, this species has been found in considerable numbers by Dr. Allee and his students, who have observed that it occupies very tiny burrows in the *F. ulkei* nests. Its relation to *F. ulkei* is not clear.

However, a considerable array of species other than ants have been obtained from the ant nests. Attention has already been called to the finding of wooly aphids during the winter and to the attendance of workers on aphids

TABLE III. *List of the co-inhabitants of F. ulkei nests*

Species	Dates
ANNELIDA	
<i>Helodrilus caliginosus trapezoides</i>	Jan. 13, Apr. 22.
<i>Octolasmus lacteum</i>	Dec. 13, Jan. 13, Jan. 24, Mar. 20, Apr. 11, Apr. 22.
CRUSTACEA	
<i>Tracheoniscus rathkei</i> Brandt	Dec. 13, Jan. 3, Jan. 13, Jan. 24, Feb. 15, Mar. 20.
<i>Eucrangonyx gracilis</i> Smith	Feb. 15. From soil water at bottom of nest.
<i>Cyclops bicuspidatus</i> Claus	Feb. 15. From soil water at bottom of nest.
ARACHNIDA	
<i>Agelena naevia</i> Walck.	Feb. 3.
<i>Cicurina brevis</i> Emerton	Mar. 7.
Spider eggs	Feb. 7, July 23.
MYRIAPODA	
<i>Nadabius iowensis</i> Meinert	Dec. 13, Jan. 3, Feb. 3, Feb. 7, Mar. 7.
<i>Pokabius bilabiasus</i> Wood	Jan. 24, Feb. 24.
<i>Scutigera immaculata</i> Newport	Jan. 3.
<i>Arenophilus</i> sp.	Jan. 3.
<i>Brachygeophilus embius</i> Chamberlin.....	Feb. 15.
<i>Scytonotus granulatus</i> Say	Feb. 24.
<i>Parajulus venustus</i> Wood	Feb. 7, Mar. 7.
COLLEMBOLA	
<i>Entomobrya</i> sp.	Dec. 2, Jan. 24, Feb. 7.
HOMOPTERA	
Wooly aphids (undetermined)	Oct. 11, Nov. 1, Jan. 24, Feb. 3.
Cicada nymphs	Dec. 13, Apr. 11.
Neuroptera pupa (<i>Chauliodes</i> ?)	June 18
ORTHOPTERA	
Roach nymphs	Dec. 13, Jan. 24, Feb. 3, Mar. 7, Mar. 20, June 26.
COLEOPTERA	
<i>Tachys incurvus</i> Say	Feb. 15, Mar. 7, Apr. 22. Crawling on surface of mound, Apr. 22.
<i>Harpalus pleuriticus</i> Kirby	Feb. 24.
<i>Amara polita</i> Lec.	Apr. 11.
<i>Lachnosterna</i> sp. (adults)	Dec. 13, Jan. 3, Feb. 7, Apr. 11.
<i>Lachnosterna</i> sp. (larvae)	Dec. 13, Feb. 7, Apr. 11.
<i>Batrissodes globosus</i> Lec.	Feb. 15. Other specimens of pselaphids taken on Dec. 2 and 13, Jan. 13 and 24, and Feb. 3.

- Batrissodes spretus* Lec. Mar. 20.
Megastilicus formicarius Casey Feb. 3. Other specimens of staphylinids
 taken on Nov. 1, Jan. 24, and Feb. 15.
 Undetermined coleopterous larvae Dec. 13, Apr. 2.

DIPTERA

- Microdon* sp. (larvae) Nov. 22, July 14.

HYMENOPTERA

- Amblyteles seminiger* Cress Jan. 3.
Myrmica scabrinodis Nyl. Apr. 11, July 24. Among lab. ants, but
 origin uncertain. Probably collected
 with *F. ulkei* workers from nests in
 the field.
Crematogaster lineolata Say Oct. 11. Found on surface of mound.
Lasius (Acanthomyops) interjectus Mayr. June 18.

in the summer. *F. ulkei* is an aphidicolous species like so many others of the same genus. In addition to the above, pselaphid beetles (*Batrissodes globosus*, and *B. spretus*) were collected; other undetermined individuals were found throughout the winter. The same is true of the staphylinid beetle, *Megastilicus formicarius*. Two specimens of the larvae of *Microdon* sp. were taken from the nests, one on November 22, and the other on July 14. These species represent various relations of dependence upon the ants from friendly to persecuted. Of doubtful relationship to the ants is the carabid beetle, *Tachys incurvus*, which was found on several occasions in the nest and also crawling on the surface of the mound. This beetle is known to occur in ant nests, but lives in other environments as well.

All the rest of the species listed in Table III probably represent individuals attracted to the burrows in fall-for over-wintering purposes. The majority of the species in Table III come under this category. They are able to gain access to the nests because of the early retirement of the ants into hibernation and the consequent reduction of activity in the nest. Very few of these species have been taken in the summer; they are undoubtedly driven out of the nests in the spring when the ants resume activity.

A large, deserted *F. ulkei* nest was opened on February 7. This nest was partially overgrown with turf, but the ant burrows were still intact. A large number of species of animals, ranging from annelids to Hymenoptera, had taken possession of this nest for hibernation. The general similarity of these animals to those listed in Table III further substantiates the fact that most of the species listed in Table III are mere hibernants that are attracted to the ant nests by the availability of hibernation quarters in the nests.

Attention has already been called to the wholly unexpected discovery of the two species of aquatic crustaceans (*Eucrangonyx gracilis* and *Cyclops bicuspidatus*) in the soil water of the nests. Two individuals of the former and one of the latter were found February 15. Of course, these species do not come in contact in any way with the ants, but are merely given in Table

III as having been taken in the ant nest, or more correctly stated, below the ant nest.

SUMMARY

A number of experiments and observations on the behavior, habits and life history of the mound-building ant, *Formica ulkei* Emery, are here reported. These have come to light incident, to a more detailed study of the over-wintering phases of the life history, which will be reported in a later publication. The following points are brought out in this paper:

1. A correction is offered in the description of the male: The mandibles are 3-toothed instead of edentate as described by others.

2. The species is largely confined to the Canadian zone. It has been reported from only a few scattered regions in the Transition zone. In the Chicago region it occurs only at Palatine and at Palos Park, Illinois. It is found in open, oak-elm-hickory woods situated on low hills with low areas scattered throughout the woods.

3. The species nests in the soil, and builds rounded or conical mounds that often attain considerable size (the largest was nine feet in length and almost as wide). The mound is much burrowed out, composed of excavated earth (mostly clay), and covered with a thin crust of a mixture of earth, roots, small twigs, dead blades of grass, etc. The burrows extend down to soil water level (1-5 feet below the surrounding level). No essential differences were noted in the architecture of the nests located on high and low ground except that the burrows extended deeper into the ground in the former than in the latter.

4. Activity begins in the spring as soon as frost is out of the ground. The wingless females and the workers are the only stages which hibernate.

5. Egg laying begins toward the close of April and ends the latter part of May or early June. In the observations here reported, they were laid in groups of 1-51 eggs. The egg laying proceeded in rhythms of activity, a large batch alternating with smaller ones. Each female laid 126-190 + eggs during the egg laying season in nests in which the eggs were removed as soon as laid. In two other nests in which the eggs were not removed in this way, only about 50 eggs were laid by each female.

6. The time of hatching is 9-16 days with an average time of 12.5 days. Only 1 larva succeeded in pupating in observation nests; in this instance, the length of larval life was 21 days. However, larvae were found in the nests until the latter part of August. No data were obtained on the length of the pupal life. Worker pupae were first found in the nests in the field on June 18, and callows were first taken in small numbers on July 23. Worker pupae continued in the nests until October 21. The large male and female pupae were first found on July 8, and on July 14 the first winged males and females were obtained in the field.

7. The nuptial flight was not seen. But indirect evidence seems to indi-

cate that mating took place very close to July 20. If a nuptial flight takes place at all, it is in all probability very limited in extent.

8. Some of the ants had begun hibernation by September 10, but surface activity did not cease until the early part of November. The winter is spent in the deepest part of the nest just above soil water level. Here the ants are aggregated into very densely packed masses. They are very sluggish during this time, but maintain enough activity to be able to crawl to cover slowly when disturbed.

9. Considerable difficulty was encountered in the rearing experiments because of the cannibalistic habits of the ants. Largely as a result of this, only a small percentage of the eggs hatched and only one larva pupated.

10. A large number of eggs were laid by workers. Even mature females appeared in the nests stocked only with workers originally. The virginity of these workers cannot be vouched for.

11. The ants get along very well in the laboratory on a diet of fruit, honey and other sweets, and other insect bodies. Regurgitated food is fed the young and also the adults. All castes have been observed to feed directly upon the food offered in the laboratory nests. Foraging activities carry the workers into the surrounding regions for an observed distance of 57 feet.

12. The well known solicitude for the various members of the colony is shown by the workers. The young are carried about in accordance with the changing conditions of the nest. They are fed and otherwise cared for. They are sorted according to age. The pupae seem to be kept closer to the surface than the larvae. Much time and energy are expended on keeping the females immaculate. The transport of workers by other stronger workers has been observed on several occasions.

13. In its relations with other species of animals, *F. ulkei* is not an aggressive or slave-making species, but it defends its nests with great vigor. The workers possess a powerful means of defense in the ability to secrete formic acid, the fumes of which are toxic enough to kill the ants themselves when confined in a narrow space. In consequence of this energetic defense of the colony, very few specimens of other species of ants were found in the nests. A number of aphids, pselaphid and staphylinid beetles and *Microdon* larvae were found in the nests. Besides these myrmecophiles, a large number of other species of invertebrates, ranging from annelids to Hymenoptera, were observed inhabiting the ant nests in winter for the purpose of hibernation.

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FIG. 1. Females (*a*), workers (*b*) and eggs (*c*), enlarged about four times. The picture was taken May 23, 1925. Some of the bodies are covered with droplets of water due to the necessity of cooling the ants on ice to keep them quiet long enough to get a picture.

FIG. 2. Various life history stages, natural size. The picture was taken July 26, 1926. (*a*) Winged female; (*b*) winged male; (*c*) and (*d*) wingless females; (*e*) group of five workers; (*f*) three cocoons of males or females; (*g*) twelve worker cocoons; (*h*) ten larvae in various stages of development.

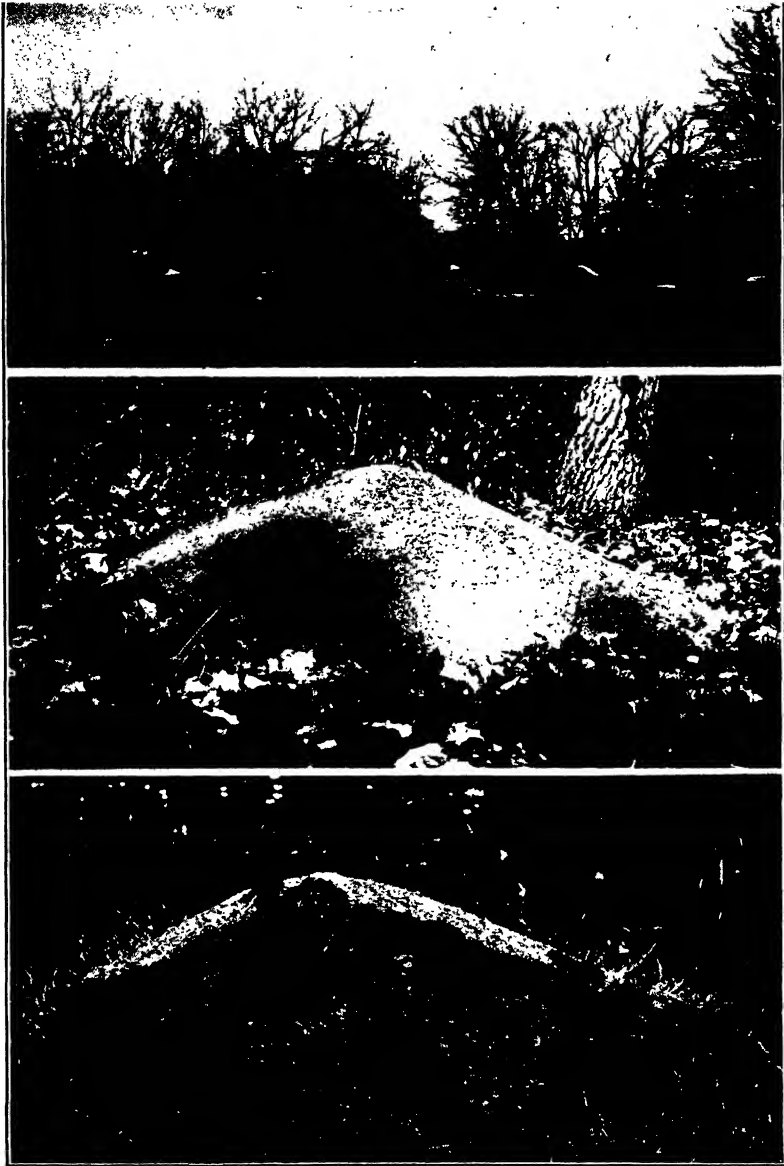


FIG. 1. Showing the distribution of colonies along the border of a low spot in the woods at Palos Park, Illinois. The picture was taken Feb. 12, 1925, the day after a light fall of snow. By noon, all the snow had melted except on the shaded side of each mound; thus the remaining snow sets off the mounds from the rest of the surroundings. Five colonies are indicated by the white spots.

FIG. 2. Large mound at Palatine, Illinois. Picture taken Oct. 11, 1924. The surface is seen to be strewn with debris of various kinds, and is without grassy covering.

FIG. 3. Large mound seen in cross-section and showing architecture of mound. Picture taken Aug. 14, 1926 at Palatine, Illinois. The mound was cut in two with a spade down to surface level. The surface crust, composed of mixed debris and soil, may be seen; also the galleried interior of the mound.

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RELATION OF THE MEADOW MOUSE *MICROTUS P. PENNSYLVANICUS* TO THE BIOTA OF A LAKE CHAMPLAIN ISLAND

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INTRODUCTION

The presence of mice on Sloop Island, Lake Champlain, New York, was noticed by the closely cropped grass and the maze of interlacing burrows and runways covering the surface of the vegetated area. Because of the possibility of determining some of the relations existing between the sole mammalian species of the island and the other species of animals and plants, the writer has attempted a complete survey of the macroscopic biota of the island. The notes were obtained while engaged in certain field work for the Roosevelt Wild Life Forest Experiment Station, Syracuse.

METHODS

Metal box traps were placed on the island for a total of twenty trap-nights. This was without doubt trapping enough to secure every mouse there. The adults and one of the young mice obtained were preserved and identified by the writer as the common meadow mouse [*Microtus p. pennsylvanicus* (Ord.)].

An effort was made to secure specimens of each of the macroscopic animals on the island, but three species of spiders are known to have avoided capture, and probably a few arboreal insects escaped unnoticed. Certainly all abundant forms were obtained.

The orthoptera were identified by T. H. Hubbell, of the University of Florida; the ants by F. M. Gaige, of the University of Michigan, the snails by Miss Mina Winslow also of the University of Michigan; the sow bugs by W. G. Van Name of the American Museum of Natural History; mosses, lichens and liverwort by L. H. Pennington of the New York State College of Forestry. For the identification of other plants the author alone is responsible. Slugs were too badly damaged in transit to admit identification.

All burrows of the mice that could be uncovered were examined. Some others went into crevices in the solid rock and could not be reached. All notes were made during the first two weeks of September, 1926.

SLOOP ISLAND

Sloop Island is a small rocky satellite of Valcour Island, Lake Champlain, New York, lying but six hundred feet off the point between Paradise Bay

and Sloop Bay. To the east there is a two and three quarter mile expanse of open water between Sloop Island and Grand Isle, Vermont. During periods of low water, Sloop Island is but one hundred and ninety feet long and one hundred and thirty broad. Its total area is about 12,350 square feet. The rock rises abruptly from the water, except to the east, to a height of about ten feet. The island is supposed to have gotten its name during the Battle of Lake Champlain when, according to tradition, it was fired on, being mistaken for a sloop when visibility was poor.

The formation is dolomitic limestone of the middle Chazy beds, deeply furrowed by glaciers.

The prevailing wind is from the south, and from this direction may attain a high velocity. Such winds, lasting for several days, keep the lake very rough and effect the transportation of a small quantity of beach drift. Elements of the island's population arriving by driftwood or other floating debris would be most likely to come from this direction. Access over the winter ice is most direct from Valcour Island.

VEGETATION

That portion of the island which bears soil and plants is limited to an area ninety feet long and twenty five feet wide, a surface of but 1,100 square feet. The remainder of the island is of barren rock, exposed to wave and ice action, and hence incapable of supporting soil or plants.

The most conspicuous elements of the small patch of vegetation which crowns the island are five mature arbor vitae (*Thuja occidentalis*) and one balsam poplar (*Populus balsamifera*). A few small aspens (*Populus tremuloides*) are the only other trees. Mullein (*Verbascum Thapsus*), raspberry (*Rubus idaeus* var. *aculeatissimus*) and grasses (*Poa pratensis* and *P. annua*) constitute the bulk of the remaining flora.

A complete list of the plant species follows:

TREES

Thuja occidentalis L., arbor vitae, five mature trees; *Populus balsamifera* L., balsam poplar, one mature tree; *Populus tremuloides* Michx., quaking aspen, few small trees.

SHRUBS

Rhus typhina L., staghorn sumach, abundant; *Cornus circinata* L'Her., round-leaved dogwood; *Symphoricarpos racemosus* Michx., snowberry; *Shepherdia canadensis* (L.) Nutt., buffalo berry; *Amelanchier canadensis* (L.), Medic., shadbush; *Arctostaphylos Uva-ursi* (L.) Spreng., bearberry; *Sambucus racemosa* L., red-berried elder; *Rubus idaeus* var. *aculeatissimus* (C. A. Mey.) Rehl and Tiling, wild red raspberry, abundant.

HERBS

Verbascum Thapsus L., mullein, common; *Achillea Millefolium* L., yarrow; *Aquilegia canadensis* L., columbine, common; *Smilacina stellata* (L.) Desf., false Solomon's seal; *Epiplobium angustifolium* L., fireweed; *Campanula rotundifolia* L., harebell; *Solidago juncea* Ait., goldenrod; *Fragaria vesca* var. *americana* Porter, strawberry; *Poa pratensis* L., Kentucky blue grass, abundant; *Poa annua* L., low spear grass, abundant; *Leptilon Canadensis* (L.) Britt., fleabane; *Arenaria stricta* Michx., rock sandwort; *Cirsium arvense* (L.) Scop., Canada thistle; *Arabis brachycarpa* (T. and G.) Britt., purple rock cress.

MOSESSES

Ceratodon purpureus (L.) Brid.; *Tortula mucranifolia* Schwaegr.; *Thelia hirtella* (Hedw.) Sulliv. (?); *Dicranum scoparium* (L.) Hedw.

LIVERWORT

Porella platyphylla Lindb.

LICHENS

Cladonia pyxidata (L.) Hoffm.; *Cladonia* sp.

INVERTEBRATE ANIMALS

All the invertebrates collected were confined to the vegetated area and dwelt under flat rocks or in the burrows of the mice. The paucity of species is without doubt correlated with the small number of plant species on the island and with the lack of suitable breeding places for a wide variety of forms. Those species which were common had apparently found little competition, for their numbers were legion. Especially was this true of the cock-roaches which occurred in scores under every flat rock.

It could not be determined which if any of these species were used as food by *Microtus*. It can be said of course that an abundant food supply was here available, but that the great numbers of individuals made it seem that the mice were not using these other animals as food, or that there were too few mice to hold the insects and others in check.

The species taken are:

ORTHOPTERA

Gryllus assimilis Fabricius, field cricket, abundant; *Parcoblatta pennsylvanica* (DeGeer), wood roach, abundant; *Ceuthophilus terrestris* Scudder, woodland stone cricket, abundant.

HYMENOPTERA

Lasius niger Linn. var. *americanus* Emery, ant, abundant.

ARACHNIDA

Three species of spiders, unidentified, common.

CRUSTACEA

Cylisticus convexus (DeGeer), sow bug, common.

MOLLUSCA

Succinea ovalis Say, common; *Anguispira alternata* (Say), common; *Agriolimax* sp., common; slugs, common.

VERTEBRATE ANIMALS

There are no resident amphibia or reptiles.

Many birds visit the island occasionally, but probably play no important role in bringing food to the mice or in competing with them for food. Sea gulls might occasionally bring dead fish to the shore which could be used for food.

Muskrat, mink and otter might be expected to visit the island occasionally in the summer, while many other mammals probably pass over or near it in the winter. Carnivores would have easy access to the island over the ice from Valcour Island.

Man visits the island occasionally but has little influence on the fauna (scientists excepted) unless it be to leave a few scraps of food which would by no means be sufficient to support even one pair of *Microtus*, especially since the few visitors come in the season of plenty.

MICROTUS

Seven *Microtus* were taken from this quarter acre island. They were all in good condition, yet they had but 1,100 square feet (the area of vegetation) on which to live. Each mouse had the equivalent of but a little over a twelve foot square to feed from, and at that a square which was far from being typical of situations in which *Microtus* reaches its maximum abundance.

The two adults resident on the island were of average measurements for their species, and weighed as much as specimens from Valcour Island where conditions are rather favorable. The male weighed 48.8 grams and the female 42.2 grams. The testes were large (16 mm. long) though the female evidenced no sign of breeding activity as she neither contained embryos nor showed signs of lactation.

The young were fairly uniform in size and weight, apparently being of one brood. The longest had a total length of 141 mm. and the shortest (though heaviest) a length of 115 mm. The lightest weighed 16.1 grams and the heaviest 25.0 grams.

If, as the writer supposes, the young were all of one litter then the female must have given birth to but one brood during the year up to the middle of September, or else earlier broods were lost through food shortage or other mishaps.

The meager evidence would suggest that one pair of adults crossed to

Sloop Island from Valcour Island over the ice during the winter of 1925, though of course the two adults may have been merely survivors of a wave or of a previous year's population. They may, too, have arrived independently over the ice or by accidental carriage on logs.

FOOD OF *MICROTUS*

There were in early September but two principal sources of food for the mice. Of these perhaps the most important at the time was the mullein. It was observed that all of these plants on the island, with the exception of a few then in flower, were cut down and into lengths of six to ten inches. The leaves were removed in part, and eaten by the mice. The heads of each stalk had been removed but were not visible on the surface of the ground. The empty seed pods and flower heads of a few mullein were found in the burrows of the mice. Most of the cut lengths were left at the point of cutting, though some had been dragged into the entrances of the burrows. A ring of teeth marks about half way up a standing mullein suggested that they were not first felled from the base.

Blue grass (*Poa pratensis*) and low spear-grass (*P. annua*) formed the second most important item of the microtine diet, and was without doubt important during the greater part of the year. Over the whole area the grass was very closely cropped, both as to leaves and seed heads. It was in fact difficult to find good specimens for identification. Blue grass was the more common of the two species present. The one vestige of a mouse nest found was constructed of this grass.

The basal leaves of the goldenrod were also eaten. A fourth plant, too young and too damaged to identify was found to be eaten almost in entirety. The species was not common on the island.

Of the many sumach on the island but one was found girdled and killed, and this had occurred some months before the observation was made. There were no signs of present utilization.

Examination of the list of plants given earlier reveals the presence of several other species that possibly contribute at least fruit to the welfare of *Microtus*. Such are the strawberries, bearberries, snowberries, red-berried elder, raspberries, etc.

It is not improbable that the mice have entirely eliminated one or more species of the island's flora.

RUNWAYS

The runways of the mice were everywhere visible as winding denuded grooves in the soil running from one burrow to a crevice or to another burrow. The grass was in all cases too short to arch over these paths. The burrows usually ran into crevices or under flat rocks since the soil was in most places too thin for tunneling. They were barren of extraneous matter except

for the occasional scattered midden of mullein or grasses, and the presence of invertebrate animals.

Within five feet of the spot where all the young animals were secured was found a badly worn grass nest, occupying a slight concavity under a large flat rock. The adults were caught about sixty feet from this nest the first night the traps were out.

SUMMARY

A pair of adult mice, *Microtus p. pennsylvanicus*, and five equal aged juveniles of this species were the only vertebrates occurring on Sloop Island, Lake Champlain, New York, in September 1926. It is not known in what manner they reached this spot.

The vegetated area of the island was confined to one hundred and twenty square yards at the summit of the rocks. Here the mice were feeding principally upon common mullein, *Verbascum Thapsus*, grasses, *Poa pratensis*, *P. annua*, and the basal leaves of a golden rod *Solidago* species. The island presented a very closely cropped appearance. Several species of invertebrates were common, though they are not known to have been utilized as food.

One nest was found. Open runways connected the covered passages of the rock crevices.

It is improbable that all of these mice could find food enough on the island to last through the winter, or even until the ice on the lake permitted their escape or their destruction by a foraging carnivore.

REVIEWS

SOIL MICROBIOLOGY ¹

In the preface to his "Principles of Soil Microbiology" the author states what he feels should be included in a book on the subject. "A study of the occurrence of microorganisms in the soil, their activities and their rôle in soil processes." . . . "This book is a collection of known facts concerning microorganisms found in the soil and their activities; it is a study of the literature dealing with the science in question; it is an interpretation of the facts already presented; it indicates the various lines of investigation and notes where further information is especially wanted. Soil microbiology is a science which is at the very base of our understanding of agricultural processes and the practice of agriculture; it comprises a number of sciences." . . .

One cannot read this book without being impressed with the extensive character of the work and the thorough-going manner in which the author has presented the results of the great number of investigations in soil microbiology. Some idea of the magnitude of the task which Waksman has performed so well may be gained from the number of original papers reviewed, approximately 2,500. In this vast number of references to the literature presented in this book, it is especially gratifying to find that the author has reviewed the work of the Russian soil scientists and other foreign workers whose publications are not as readily accessible as those in the English, French and German.

Waksman's book represents a comprehensive account of the information available in soil microbiology. Never before has there appeared in the English language such a detailed collection and summary of the results of researches in soil microbiology.

The volume is divided into four main sections:

Part *A*. Occurrence and Differentiation of Microorganisms in the Soil.
One chapter.

Part *B*. Isolation, Identification, and Cultivation of Soil Microorganisms.
Thirteen chapters.

Part *C*. Chemical Activities of Microorganisms. Nine chapters.

Part *D*. Soil Microbiological Processes and Soil Fertility. Nine chapters.

Although the book is primarily a guide to research workers and teachers in soil microbiology and related subjects, rather than a text book, it will be found of great help to graduate students.

As stated in the preface, the author has attempted not only to collect the

¹ Waksman, Selman A. Principles of Soil Microbiology. xxviii + 897 pp., 19 pls., 82 figs., Baltimore, Williams and Wilkins Company, 1927.

literature relating to soil bacteriology, but also to make an analysis of the situation as it exists today. In general, this analysis has been made exceedingly well. There are, however, certain exceptions; *e.g.*, conflicting viewpoints are given on some phase of the subject and the author has not indicated in any way what he considers the true concept. A few examples will illustrate this point:

In the discussion of anaerobic nitrogen fixing bacteria the definition of the *Bac. amylobacter* group is not clear. On page 106 the author refers to *Clostridium*, *Amylobacter*, and *Granulobacter* groups and also mentions "other butyric acid bacteria," while on page 109 he quotes Bredemann as grouping all butyric acid bacteria under the name *Bac. amylobacter*. On pages 110 and 175 *Bac. amylobacter* is said to be rare in acid peat soils, but on page 111 it is stated that *Cl. pastorianum* can withstand considerable acidity and consequently may be abundant in acid soils. The author on p. 104 gives the impression that *Cl. pastorianum* and *Bac. amylobacter* are synonymous.

The statement from Vogel and Zipfel, reference 133, page 130, concerning the value of the agglutination for the isolation of the root nodule bacteria from soil, is misleading.

Another example is found on pages 132 and 133. "The soybean organism was reported by some as possessing peritrichic flagellation but by most other workers as monotrichous. The differences thus obtained were due either to the fact that cultures of various ages were employed or different types of bacteria exist, even for the same plant (as *Soja max*), in different parts of the world." On page 133 it is stated that "organisms obtained from nodules of different species of plants belonging to one genus have the same type of flagellation."

Again on page 138 it is stated that "The nodules of *Alnus*, *Elaeagnus* and *Ceanothus* were found to be caused by bacteria belonging to the *Bact. radicola* group and capable of fixing nitrogen." While on page 139 the report is different. "Burrill and Hansen came to the conclusion that the root nodules of *Ceanothus* (*C. americanus*), *Alnus*, *Cycas revoluta*, and *Myrica* are not caused by *Bact. radicola*."

The presentation of the statements as found in the scientific literature may be the only feasible method for the author to follow, and yet it is a difficult matter for the reader to judge what is the best evidence. Because of Waksman's intimate knowledge of the subject, the reviewer feels that some expression of opinion would have been desirable.

The organization of the subject matter is good and logical. However, the plan adopted by the author, and the very complete manner in which he has executed it, have resulted in repetition. For example, directions for making silica gel medium are given in three places, pages 11, 68 and 196.

In general, the book is well printed and the illustrations good. Due to the nature of the publication—the enormous number of papers reviewed—

it is not surprising that there are certain errors in the references, and it is hoped that in the next edition these errors whether in the manuscript or in typography will be corrected. Some of the examples of typographical errors are noted in the chapter relating to nitrogen fixation, pages 119 to 133, reference numbers 73, 77, 85, 110, 132, and 133. The reference 20 on page 823, Fred. E. B., Peterson, W. H., and Davenport, A., Jour. Biol. Chem., 42: 175, 1920, should read Wright, W. H., The Nodule Bacteria of Soybeans: I. Bacteriology of Strains, II. Nitrogen-Fixation Experiments, Soil Science, 20: 95-141, 1925.

On page 136 the author has quoted from the first edition of Bergey's "Manuel of Determinative Bacteriology," 1923, with reference to the classification of the legume nodule bacteria. This classification was manifestly incorrect and corrections were made in the second edition of the manuel which appeared in 1925.

Waksman has made an excellent and thorough selection of the books for reference. This part of the book will be found of great value, especially for the research worker in Soil Microbiology. In a few cases reference has been made to old editions; *e.g.*, Fuhrmann, 1913, Kayser, 1921, and Russell and Hastings, 1915, have all appeared in later editions.

The plates are, on the whole, good, although the numbers *B* and *D* of Plate VII (facing p. 122) are inverted. The line drawings and graphs are in some cases so small that it is difficult to read the figures. (See the cuts on pages 4, 678, 679, 747, 756.)

The volume is fully indexed under the headings of both authors and subjects, and thus becomes a most convenient reference work. There can be no doubt of the great value of this important work for the investigators of soil problems. Waksman is to be congratulated on the way in which he has handled the difficult task of collecting and summarizing the results of research in soil microbiology.

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ROOTS OF VEGETABLE CROPS ¹

Root growth at different stages in the life of the plant, and under varying environmental conditions, is yearly becoming less of a mystery. Opaque soil has been lifted and removed and the still more difficult, though physically less arduous task of correlating the various experiments and recording them in unified reports, thanks to Dr. Weaver and his faithful cohorts, goes on at a rapid pace.

The latest publication, "Root Development of Vegetable Crops,"¹ deals

¹ Weaver, John E. and Bruner, Wm. E. "Root Development of Vegetable Crops." Pp. xiii + 351, New York, McGraw Hill Book Co., 1927.

with more than thirty of the plants grown in the market gardens of the United States. Thus in the present volume and in its predecessor, "Root Development of Field Crop,"² practical ecology applied to economic plants has been developed from the long series of studies made upon roots, beginning with this author's earlier books, "Ecological relations of Roots," and "Root development in the Grasslands Formation."³ It is easy to foresee that vegetable gardeners will derive much information of interest from a study of the principles of root adaptation to cultural practices and the interrelations of plant activities to climatic and soil conditions. Each chapter devoted to a separate vegetable crop contains a summary with practical suggestions for cultivation based upon the root studies. Equally will ecologists enjoy using the simple authoritative descriptions of the progress of root growth. As in the previous volumes there are numerous plates containing diagrams of roots drawn to scale to show depth of penetration and lateral spread, as well as the correlation of the root activity with the entire plant's development.

The book is essentially what a lawyer would describe as a case book. With only a minimum of space devoted to a discussion of the conditions of growth at Lincoln, Nebraska, and Norman, Oklahoma while the experiments were in progress, the reader is at once led to examine the roots of the crop plants studied. A chapter is devoted to each species, though in some cases outstanding varieties having been studied, the results are carefully but briefly contrasted and compared. In Copenhagen Market cabbage (p. 101) a first examination of the plants was made when they were 55 days old. The plants were 5 inches high with 20-25 leaves and with a transpiring area, considered as the sum of the upper and lower leaf surfaces, of nearly 3 square feet. "In all of the several plants examined a main root arose from the base of the enlarged underground part (the taproot having been destroyed in transplanting) and ran in a somewhat tortuous downward course. These roots reached maximum depths of 38 inches. Most of the laterals ran outward and downward, . . . to depths of 6 to 8 inches. At this depth many pursued a rather horizontal course in the second 6 inches of soil. They frequently had a lateral spread of 3 feet. . . . Few branches arose in the surface 2 to 3 inches of soil. The main lateral roots, usually 22 to 28 in number were only fairly well clothed with branches. . . . Since practically no roots occurred in the surface 6 inches of soil, except near the plant, cultivation at this time would have resulted in a minimum of root injury." On p. 107 we find that, "When the taproot is injured in transplanting, one of the long laterals usually assumes the position of a taproot. It is usually no more prominent, however, than

² Weaver, John E. "Root Development of Field Crops." New York, McGraw Hill Book Co., 1926.

³ Weaver, John E. "The Ecological Relations of Roots." Carnegie Inst. Wash., Publ. 286, 1919.

Same author. "Root Development in the Grassland Formation." Ibid., 292, 1920. For review of these two publications, see *ECOLOGY*, 2: 145-149, 1921.

many of the other major laterals that arise in great numbers from the base of the enlarged underground part. . . . A maximum lateral spread of 3.5 feet is attained about the time the heads are two-thirds grown. . . . Mature plants have a working level of 5 feet, to which depth the soil is well ramified with a profuse network of absorbing rootlets. Thus a single plant draws upon more than 200 cubic feet of soil for water and nutrients." It would be interesting to compare these results with others taken in more humid stations nearer the Atlantic seaboard.

In contrast to cabbage some quotations from the summary on lettuce (p. 327) will do as much as anything that the reviewer might be able to say in pointing out the reference value of this book. "Lettuce has a taproot which grows very rapidly, sometimes at the rate of 1 inch per day, especially in loose moist soil. The first laterals are horizontal and very near the soil surface. All of the very numerous, large laterals, . . . originate in the surface 10 inches of soil. . . . Before the middle of June, the well branched root system thoroughly occupies the soil to a depth of 2 feet. The taproot extends nearly 2 feet deeper. . . . On maturing plants the roots extend their working level to about 5 feet, and maximum depths of over 6 feet are attained. From just beneath the soil surface to deep into the subsoil networks of fibrous rootlets are abundant. These are densest in the surface foot of soil." Compacted, poorly prepared soil is probably a more serious detriment to the production of crisp tender lettuce than is hot dry weather. I remember having seen a gardener with a greenhouse attempting for a couple of years to grow lettuce for the winter market in his greenhouse benches where the roots were in not more than eight inches of soil warmed beneath by the hot water pipes under the benches.

Transplanting.—Weaver discusses the work of Loomis, Crane-field, Myers and others, and uses it to supplement the experiments. These experiments have shown (p. 119) that "the general effect of transplanting is to retard development. . . . The degree of retardation varies with the kind of plant, its age and the conditions of transplanting. Cabbage is one of a group of plants, in which are also included tomatoes, lettuce and beets that easily survives transplanting. Peppers, onions, celery and carrots are transplanted with more difficulty and a third group consisting of such species is corn, beans, melons, and cucumbers are very difficult to transplant successfully except at a very early age. . . . A single transplanting at a later stage of development may do more injury than two or three earlier transplantings. . . . There is a rapid decline in the rate of root replacement with increasing age."

Diseases.—The important field of the relations between root environment and diseases has not yet become a part of Weaver's experimentation, the subject which is introduced only for cabbage and squash is not even indexed, and is treated from the pathological viewpoint, that is not as a part of the general environment of the plant. Crop sanitation in the future will have

to study roots more fully and examine the relations between environment and disease.

The prominently skeletal structure of the book—one chapter for each crop plant and one for the introduction—is rigidly adhered to, even in the index. To the reviewer at least, it seems as though the whole book would have benefitted if space had been devoted to an enlargement of the introduction into several chapters with some clue to the effect of environmental factors. Doubtless, valuable data would have been sacrificed, but a more complete union of principles and their application would have been the result. It is a doubtful compliment to the taxonomists to have the thirty three vegetable crops presented in systematic order beginning with corn and onion for the monocotyledons and ending with lettuce for the dicotyledons, when an alphabetical arrangement would have served.

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PLANT ECOLOGY

Ecology is perhaps the only phase of plant science not over-burdened with elementary text books; in fact, up to the present time textbooks devoted to plant ecology have been conspicuous by their scarcity. This makes the recent volume by McDougall¹ decidedly welcome, and it should find for itself a place in junior colleges, normal schools, and possibly in some high school classes. In it the author has attempted to cover the entire field and with considerable success.

The first 50 pages discuss the ecology of roots, stems, and leaves; the following 90 pages consider various sorts of symbiosis; 50 pages are then devoted to such factors as light, heat, air, soil, and water; and then comes a discussion of plant communities covering nearly 100 pages. A chapter is devoted to applied ecology, and an appendix to laboratory and field methods, while at the end of each chapter there is a useful list of references.

The author seems to have done his work well, and it is safe to predict that the book will prove a very useful addition to our text books. The style is direct and good, the illustrations numerous and well chosen, the organization simple and logical, while the data are abundant and up to date.

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¹ McDougall, W. B. "Plant Ecology." Pp. vi + 326, Figs. 115. Philadelphia, Pa. Lea and Febiger. 1927.

PLANT ECOLOGY OF PORTO RICO¹

Ecological surveys of the tropics based upon a thorough knowledge of the species involved are comparatively rare. The present effort combines the advantages of the cooperation between practical plant ecologists on the one hand and the authors of the comprehensive "Descriptive Flora of Porto Rico and the Virgin Islands"² on the other. Ecologists have sometimes suffered from the criticism that they were studying organisms of whose identity they were innocent. How far off that criticism is in the present paper is obvious when the authors say at the beginning that all specimens upon which their work is based have been identified by Messrs. Britton or Wilson.

Porto Rico, except for a small coastal region, has been uninterruptedly out of the water since late Cretaceous time. Small changes of level have occurred and apparently are now in progress, but erosion and the establishment of such climax vegetation as the activity of this base-leveilling would permit, has been going on for a very long time. The island's early settlement, large sugar estates, and relatively dense population have all contributed, however, to the interference, the telescoping and in many cases to the destruction of that climax. It is a region, then, where conclusions are difficult to draw, and open to the constant objection, as the authors of this singularly lucid paper freely admit, that they are based on evidence which, if more complete, might change their opinion.

The island vegetation appears to divide itself into three major categories: (a) that of the northern coastal plain; (b) the central mountainous region, both of which have a copious rainfall, and (c) that of the south shore where the rainfall is as low as 60 and in some places 40 inches a year. It must be remembered that in the tropics a given quantity of rain counts for less than in cooler regions. Successional relationships have been worked out for the associations along the north and south coasts, based upon an excess of water, a deficiency of it, an excess of salt, and the average mesophytic types.

How badly erosion and cultivation have smirched the record is singularly well shown by the fact that the authors are unwilling to assign successional relationships to the five major plant associations of the central mountainous region. Perhaps no one more than the senior author of this paper is so competent to assign successional significance to these tropical vegetation types. His recent writings on the fundamental unit of vegetation, and related topics, must have made the impulse to arrange them in some paper scheme very

¹ Gleason, H. A., and Cook, M. T. "Plant Ecology of Porto Rico." Scientific Survey of Porto Rico and the Virgin Islands, Vol. VII, Pts. 1-2. 173 pp., 25 figs., 50 pls. New York Academy of Sciences, 1927. Price \$4.00.

² Britton, N. L., and Wilson, Percy. "Descriptive Flora of Porto Rico and the Virgin Islands (Spermatophyta)." Scientific Survey of Porto Rico and the Virgin Islands, Vol. V, Pts. 1-4, 1923-1924 and Vol. V, Pts. 1 and 2, 1925, and 3, 1926. New York Academy of Sciences.

strong. His failure to do so is perhaps the best evidence that tropical vegetation needs much study, and, where it has been disturbed, great care in hazarding a prophecy.

An enumeration of all the plant associations on the island is unnecessary here. They are legion, and some years ago the reviewer studied some of them along the coasts of Cuba, Santo Domingo, and in the Bahamas. That experience, a mere scratch at the surface features, serves perhaps as a point of vantage in appreciating the work done on this island by Gleason and Cook. Nowhere, not even in the accounts of the tropical strand flora of the far East, and these have been numerous and sound, have I seen such a conservative, thoroughly readable and technically satisfactory presentation of the successional relationships of a tropical strand flora as in this paper.

For the central mountainous region the authors distinguish forests at lower elevations, the moist tropical forest, the rain forest, the Sierra palm forest, and the mossy forest. For most of these they were obliged to piece together the scattered record of isolated examples which cultivation and lumbering have left. But enough has been spared for them to be able to distinguish the types, and in the case of the forests of lower elevations, to describe the merging of this with the associations along the north shore, where the two meet.

Porto Rico, like all the major West Indies, is profoundly affected by the easterly and northeasterly trades, which come off the Atlantic laden with moisture. This is precipitated on windward exposures of the higher mountains, and it is in this general zone that the authors find the "moist tropical forest" and, of course, the rain forest. *Lucuma multiflora* and *Guarea ramiflora* are the most conspicuous members of the first type, and live on a forest floor singularly lacking in humus. Lists of species are given in each type and some indication of relative frequency, but the number of species involved and the time at command made tallies such as are common to foresters impossible.

Between this "moist tropical forest" and about 2,000 feet on Luquillo Mountains occurs the rain forest, or what is left of it. The most valuable tree, *Dacryodes excelsa*, has suffered from cutting, but as in most tropical forests this makes less difference than in regions where pure stands occur. *Dacryodes* grows in small isolated colonies, and others, in relative order of abundance, but mostly scattered are: *Magnolia splendens*, *Inga laurina*, *Guarea Guara*, *Miconia tetrandra*, *Manilkara nitida*, *Tabebuia pallida*, *Micropholis garcinifolia*, *Coccolobis rugosa*, and many others less common.

Above the rain forest, that is above 2,000 feet, occur forests characterized by the Sierra palm (*Euterpe globosa*), which is much more generally distributed than the rain forest itself, being found, apparently as the result of an altitudinal control, over all of Porto Rico having the necessary elevation.

But above everything else—water-soaked, fog-blanketed, and wind-swept

—is the mossy forest. Its characteristic species are *Weinmannia pinnata*, *Ocotea spathulata*, *Eugenia boqueronensis* and *Tabebuia rigida*. Its ecological structure is overwhelmingly homogeneous, epiphytic and terrestrial habits being merged by mosses that grow indiscriminately on tree trunks and on the ground.

While their paper is wholly descriptive, the authors state on page 39, that there is "increasing transpiration by greater exposure to wind." That statement will not pass unchallenged, but the reviewer welcomes it. Experiments conducted at Montauk in 1924, accounts of which have not yet been published, show clearly that plants exposed to the wind transpired more water per square decimeter of leaf surface than sheltered ones. There is, in other words, experimental evidence that the authors were justified in publishing this inference and that transpiration may not be wholly a matter of insolation. They have made many other such statements and outline plainly enough the need for such instrumental work in Porto Rico as Shreve has done in Jamaica.

The science of ecology and those interested in the distribution of vegetation types in the larger West Indian islands are indebted to the authors, for they have contributed the best account of the physiographic ecology of a tropical island that comes to mind. Their work is very much enriched by fifty full page plates of vegetation and twenty-five figures.

NORMAN TAYLOR.

BROOKLYN BOTANIC GARDEN,
BROOKLYN, N. Y.

SOIL TEMPERATURE AND FOREST COVER¹

In order to determine the effect of forest and grass cover on soil temperature at definite depths, expressed in terms of daily maxima and minima, Li has accumulated a large amount of data. Records are compared for four stations situated in the Yale Demonstration and Research Forest near Keene, New Hampshire, as follows:

(1) An artificially denuded area, (2) a grass-covered area, (3) a young white pine forest, and (4) an old white pine forest. Much space in the bulletin is devoted to a detailed description of these stations and to the tabular and graphic presentation of the temperature records taken at the soil surface and at depths of 6, 12, and 24 inches. The data affords as adequate a basis for the conclusions as can reasonably be expected. However, when it is realized that the observations, detailed as they are, cover only one growing season, the reviewer believes that a longer period of observation would have strengthened the conclusions, although they probably would not have changed them in any important particular.

The typographical make-up of the bulletin under review as a whole is

¹ Li, Tsi-Tung. "Soil Temperature as Influenced by Forest Cover." Yale University, School of Forestry, Bul. 18. 92 pp., 9 pls., 7 figs. 1926.

very good. However, the reviewer is impressed with the large number of footnote references to literature and the extent to which duplications occur in this form of citation. This duplication could have been avoided by arranging all of the literature cited in a bibliographic section at the end of the bulletin. A number of the graphs, particularly those in Figures 13, 16, 17, 18, 19, and 20, would have been greatly improved if all but every tenth line of the coordinates had been omitted.

The method adopted for measuring soil temperature in this investigation is the one described by Toumey and Stickel.² It consists essentially of standard maximum and minimum thermometers attached to a special device which is inserted in a horizontal tunnel bored in the soil at the desired depth from a soil well. The method of measuring soil temperature by means of wooden boxes³ is condemned somewhat more arbitrarily than the comparative figures given by Toumey and Stickel on their horizontal tunnel method and the wooden boxes, seem to justify. Furthermore, on rocky sites where the soil well required by the tunnel method is impracticable, the wooden boxes afford the only means hitherto devised for periodic soil temperature readings without the use of expensive soil thermographs.

The author summarizes the results and conclusions of his study in a somewhat pretentious array of 35 paragraphs. The more important conclusions only will be mentioned here.

The surface soil attained a high maximum temperature on the denuded area but cooled very rapidly at night. The forest reduced the maximum, minimum, and mean soil temperatures at all depths throughout the entire period, July 1 to October 31, except that the minimum at 6 inches was raised by the forest in October. The forest exerted a greater influence than did grass in lowering soil temperature, and both the young and the old forest had practically the same effect. The effect of the forest in raising the minimum surface temperature was mainly due to the presence of the litter, while the trees exerted little or no influence in this respect. The effect of the forest in lowering the maximum surface temperature was largely due to the presence of the forest canopy while the litter had only a small influence.

Anyone who still adheres to the rapidly waning belief that soil temperature is unimportant as a site or habitat factor, should read Li's bulletin.

C. F. KORSTIAN.

• APPALACHIAN FOREST EXPERIMENT STATION,
ASHEVILLE, N. C.

² Toumey, J. W., and Stickel, P. W. "A New Device for Taking Maximum and Minimum Soil Temperatures in Forest Investigation. *ECOLOGY*, 6: 171-178. 1925.

³ Moore, B., Richards, H. M., Gleason, H. A., and Stout, A. B. "Hemlock and its Environment: Field Records." *Bul. N. Y. Bot. Garden*, 12: 325-350. 1924.

GERMINATION AND EARLY SURVIVAL IN OAKS¹

The vigor which our oaks display in reproducing from sprouts, and the abundance of oak in our eastern forests in spite of two centuries of cutting, burning and other abuses, might seem to render a study of oak reproduction from seed almost superfluous. Furthermore, the emphasis on white pine has caused many to look upon oaks as undesirable competitors with the pine—until the work of Fisher and his students on the Harvard Forest at Petersham² showed how to grow well formed oaks, and demonstrated the advantage of the hardwoods in mixture with the pine. However, it needs but little contact with the vast areas of run down hardwood forest, from which the chestnut has been eliminated, and only moderate foresight, to visualize the role of seedling reproduction in the future development of revenue-producing hardwood forests composed mainly of oak.

Korstian's investigation has corroborated much of the information already possessed on the seed of oaks, and added a considerable amount of useful new material.

The overwhelming importance of the biotic factor is illustrated in the enormous destruction of acorns by animals. The white oak group, chestnut oak (*Quercus montana* Wild., formerly designated *Q. prinus*) and white oak (*Q. alba* L.), seem to suffer from mammals somewhat more than the black oak group, while the latter sustain heavier losses from insect larvae, among which by far the worst offenders are the weevils. Apparently, almost the only acorns of the white oak group that escape are those concealed under the leaves. Last spring in Orange County, New York, the reviewer found an abundance of viable red oak acorns on the surface of the leaves just as the snow melted, but none of white or chestnut oak. This protection is another important function of the leaf cover which the author fails to mention in his enumeration of the advantages of this cover, which he shows reduces water loss, equalizes temperatures, and facilitates root penetration (bottom of p. 104).

It is somewhat surprising to find that the tannin content of the white oak acorn is as high as that of the red (p. 91), since it has been supposed that the smaller amount of tannin in white oak acorns is one of the reasons they have been used for food by so many animals, and even by man himself. "There is a consistently greater variation between the high tannin content of the Southern Appalachian acorns and that for the Northeast than there is between the different species." This offers a very interesting, though complex, problem in physiology and ecology.

The rates of water absorption, and of water loss, were determined for

¹ Korstian, Clarence F. "Factors controlling germination and early survival in oaks." Yale University, School of Forestry, Bul. 19, pp. 115, 7 plates, 22 figs., 1927.

² Cline, A. C. and Lockard, C. R. "Mixed white pine and hardwood." Harvard Forest, Bul. 8, 1925.

chestnut oak, white oak, black oak (*Q. velutina* Lam.) and scarlet oak (*Q. coccinea* Meunch.), and are presented graphically. The white oak shows a marked decrease in viability when the moisture content of the embryos (exclusive of fruit coats and shell) falls to between 50 to 30 per cent of their dry weight, while in the red oak the marked diminution does not occur until the moisture content has been reduced to between 30 and 20 per cent.

Sap density determinations, while few, are interesting and show the changes one would expect. The sap of white oak embryos increased, between September 1 and October 30, from 8.8 to 51.2 atmospheres, that of red oak embryos in the same period from 11.8 to 54.0.

The relation between germination and soil moisture is worked out on the basis of *available* moisture, not total moisture as is too often done. With 10.8 per cent available moisture germination was somewhat better for white and chestnut oak, than with 21.5 per cent available water. With soil 2.1 per cent below the wilting coefficient some germination took place in all four species, but the seedlings soon died. The comparison between the species in this experiment was hampered by incomplete over-ripening of the red and black oaks. It would be worth carrying this experiment further with these two oaks fully over-ripened. The different time of year at which the white oak group and black oak group germinate, the former in the autumn, the latter in the spring, caused complications in this and some of the other experiments.

The relation of temperature to germination was worked out with a series of alternating temperatures. The optimum combination was 65° F. for the day and 50° F. at night. Germination was more rapid at higher temperatures, 80° and 65°, but less complete.

One of the most remarkable parts of the bulletin, one might almost say approaching the spectacular, is the determination, by calibrated potentiometer-thermocouple apparatus, of the actual temperature in the leaves during forest fires. These temperatures are plotted graphically on page 67. Although the heat lasts only from one to three minutes, it runs from 500° to over 1,000° F., and is sufficient to kill all acorns it touches. To find the maximum heat that acorns will survive, a series of 68 tests was carried out with four species at temperatures from 140° up to 240° F., moist and dry, mostly 15 minute exposures. At 160° there was some germination, considerable in red oak, but 200° was too much for all. In decreasing order of heat resistance the acorns rank: red oak, chestnut oak, black oak, scarlet oak, and white oak least resistant.

The slower rate of germination in the black oak group led to chemical analyses (p. 88), which revealed a much higher fat content in this group than in the white oaks. The associated enzymic action, and conversion of the fats to soluble carbohydrates during after-ripening and early germination, seems sufficient to account for the slower germination in this group.

A great many different methods of storing acorns were tried, with the

result that the one recommended by Toumey,⁸ stratification in moist sand, proved best. Korstian states that the acorns should be placed below the frost line to avoid injury from freezing. The necessity for this precaution with the white oak group, on account of their autumn germination and tender radicles, is evident. But why it should be important with the black oaks, in view of their high fat content and need for after-ripening, is not clear.

The hardness of the surface soil in relation to penetration by the germinating oak roots was measured quantitatively by the use of a New York Testing Laboratory penetrometer. The limit of penetration falls between 0.01 and 0.023 mm. per gram of load applied. This work was of course done before the International Soil Congress in Washington in June, 1927, at which Prof. Albert of Eberswalde demonstrated his field instrument for determining the penetrability of forest soils. Albert showed that penetrability is correlated with productivity, easy penetration generally corresponding with favorable growth conditions. His instrument, while perhaps not reading to such a fine point as the New York Testing Laboratory potentiometer, seems better adapted for general field use.

The silvicultural methods recommended agree with those already considered best by foresters, though even greater emphasis is placed on the need for fire protection because of the vital rôle played by the leaf cover, and on the exclusion of grazing animals because of the destruction of acorns. Natural reproduction may be secured by a method of partial cutting, either selection or shelterwood.

It is a pleasure to see that in the graphs the fine lines, which reproduce as a mass of black and mar the figures in the other Yale School of Forestry bulletins (see preceding review, p. 103), have been left out. It is to be hoped that this improvement in the Yale series will be permanent.

BARRINGTON MOORE.

WASHINGTON, D. C.

⁸ Toumey, J. W. "Seeding and Planting in the Practice of Forestry." New York, John Wiley and Sons, 1916.

NOTES AND COMMENT

AN IMPROVED PAIR OF SHEARS FOR CLIPPING STUDIES ON QUADRATS

In 1925, two clipping studies were established on the Jornada Range Reserve; one of tobosa grass (*Hilaria mutica* (Buckl.) Benth.), and one of black grama grass (*Bouteloua eriopoda* Torr.). The tobosa clipping study is composed of nine one-meter quadrats, eight of which are used for clipping, the ninth serving as a density control. The eight clipped quadrats are organized into four groups of two, each pair having one plot clipped at two inches, and one clipped at four inches above the ground. In order to obtain data which will represent varying intensities of grazing, each pair is clipped at a different time from the other three, the intervals being: one week, two weeks, four weeks, and at the end of the growing season. The quadrats cut at intervals of one and two weeks produce only short flowerstalks between clippings. After the forage is air dry, it is weighed, and thus the production of each quadrat may be compared with the others, on the basis of grams of dry forage per square decimeter of tuft area.

The black grama clipping study is very similar to the tobosa study, except that the heights of clipping are one and two inches, while the clipping intervals are two weeks, four weeks, six weeks, and the end of the growing season.



FIG. 1. The improved shears in use, showing the copper side boards and adjustable gage.

In starting the studies, the question at once arose of a proper and convenient method of clipping and saving the desired vegetation. At first, a pair of small sheep shears, and later a pair of paper shears, were used for cutting the grasses, the clipped flower-stalks

being lifted with the free hand and deposited in a paper bag. This method required constant measurement to insure the proper height of grass left on the ground. Moreover, a considerable number of short flower-stalks and leaves were lost by being flipped away when cut, or lost through the inability of the operator to hold with one hand all of the vegetation clipped.

During the field season of 1927, the improved pair of shears, shown in the accompanying photograph, was developed. This instrument, made from an ordinary pair of ten inch paper shears, removes two of the outstanding faults found in the old method. The loss of leaves and short flower-stalk tips is avoided by the presence of copper strips, an inch high, soldered onto the outer edges of the blades. Another distinct advantage of this tool is the adjustable gage set on the side of one blade, whereby the necessity of continually measuring the grass is eliminated. It will be noticed in the photograph that the gage is attached $\frac{3}{4}$ of an inch from the point of the blade. It appears that flower-stalks in the midst of large tufts could be cut more easily if the gage were set near the fulcrum of the shears. The gage, which is graduated at one half inch intervals, is set at the desired height, and the clipping is begun. The gage is also equipped with a foot which prevents it from sinking into the ground, and may be slipped from its slot and clamped parallel to the blades for convenient carrying.

This instrument has been the means for a one third reduction in time of clipping grasses on the Jornada, and produces results which are more accurate in every way.

R. S. CAMPBELL AND R. H. CANFIELD.

U. S. FOREST SERVICE,
JORNADA RANGE RESERVE, NEW MEXICO.

A CONVENIENT METHOD OF BLACKENING ATMOMETERS¹

In the study of plant habitats the Livingston standardized black radio-atmmeters² are very satisfactory as a measure of external conditions influencing transpiration. Unfortunately, permanently black atmometers are not now available. The white atmometers can be blackened in various ways without appreciably changing the standardization coefficient.

A useful method is to dip the dry atmometer spheres in some sort of carbon ink—both India ink and Higgins' Eternal ink have given good results. In about a half hour, when the ink has penetrated and shows through as a blackish gray color on the inside, the spheres are placed in either aqua regia or concentrated sulphuric acid over night, so as to decompose any binding material that may have been used in the ink to keep the carbon finely divided and in suspension. After this treatment they are soaked in several changes of distilled water, to remove as much as possible of the acid.

Atmmeter cups treated in this way retain their black color very well when exposed to the weather. Several of them were used for observations of conditions in the mountain forest of the Philippines where they withstood drenching rains and strong insolation very well,³ retaining after treatment and reasonable use, the same standardization coefficient as they had before blackening. Similarly treated spheres are now in use here at

¹ Contribution 356 of the Agricultural Experiment Station, Kingston, R. I.

² Livingston, B. E. "Blackened Spheres for Atmmetry." *Science*, 58: 182-183, 1923.

Livingston, B. E. and Wilson, J. D. "A Black Collodion Coating for Atmmetry Spheres." *Science*, 63: 362-363, 1926.

³ See also Peralta, Fernando de, y Leño. "A study of the relation of climatic conditions to the vegetative growth and seed production of rice." *Philippine Agriculturist*, 7: p. 169, 1919.

the Rhode Island Agricultural Experiment Station. One of these was compared with a cup blackened with washed lampblack, with the results shown in Table I.

TABLE I. *Evaporation from white and blackened standard Livingston atmometer spheres, Kingston, Rhode Island, 1927*

Period of exposure	White sphere No. S23-318 (80) standard reading c.c.	Inked sphere No. S23-839 (80) standard reading c.c.	Surface blacked sphere No. S23-319 (81) standard reading c.c.
May 15-23.....	132.0	—	234.9 ^a
May 23-31.....	168.0	—	224.4 ^a
May 31-June 6.....	166.0	254.4	234.9 ^b
June 6-13.....	225.6	345.6	349.9 ^c
June 13-20.....	144.0	230.4	224.4 ^d
June 20-27.....	145.6	228.8	
June 27-July 5.....	209.6	322.4	322.4
July 5-12.....	126.4	190.4	193.6

The numbers in parenthesis at the head of the columns indicate the coefficients by which the spheres are to be corrected to obtain the standard readings.

^a Rains washed off the coating of washed lampblack, leaving the cup a pale gray color.

^b Rains of .64 in. on June 1, .87 in. on June 4, and .10 in. on June 5 washed off the black coating.

^c Rain on the night of June 11 washed off the black coating, but this was replaced early the following morning, so this cup was continuously black during the week.

^d Rains of .45 in. on June 24 and 1.57 in. on June 26 washed off the black coating, and though this was replaced June 25, the cup was not kept blackened as during the previous week.

The sphere No. S23-319 (81), which was blackened with a surface coating of washed lampblack, was unsatisfactory, because frequent rains removed the carbon, and left it gray or nearly white. The inked sphere, No. S23-839 (80), on the other hand gave similar readings to S23-319 on June 13 and June 20, where the latter sphere was blackened after each rain, and a much higher reading on June 6, after rains had washed the coating from No. S23-319.

Later, two inked spheres were compared. One of these was completely black, the other, No. S23-319, was streaked dark gray, due to unsatisfactory retention of the ink in some less pervious parts of the sphere. Despite this difference in appearance, the two ink-blackened spheres gave comparable readings of evaporation and insolation. Neither of these spheres, nor ones similarly treated and used in the Philippines, seemed to have their standard coefficients changed by the blackening, and this treatment made them sufficiently durable for use in locations that could not be visited more frequently than weekly for refilling.

FORMAN T. McLEAN.

RHODE ISLAND AGRICULTURAL EXPERIMENT STATION,
KINGSTON, R. I.

NOTE. Dr. Livingston has informed the Editor that spheres blackened by the McLean method above described have proven very satisfactory for humid regions, but are sometimes inadequate for arid regions such as southern Arizona, where they give too low readings for the intense evaporation which occurs in the middle of the day. The colloid lampblack coating (see footnote 2) operates very well in arid as well as in humid regions.—EDITOR.

A NATURAL ARBORETUM

An area near Moon Lake, on the Ashley National Forest, Utah, contains a complete merging of all tree species common to that region of the Uintah Mountains. Here are found trees whose habitat normally extends down to the sun-parched plains of the Basin lowlands, in association with those that reach the limits of the upper timber line.

Within a range of elevation of just a few hundred feet, and covering an area of approximately 10 acres, the following species are found.

Western yellow pine (*Pinus ponderosa scopulorum*), lodgepole pine (*P. murrayana*), limber pine (*P. flexilis*), piñon pine (*P. edulis*), alpine fir (*Abies lasiocarpa*), Douglas fir (*Pseudotsuga taxifolia*), Utah juniper (*Juniperus utahensis*), Rocky Mt. red cedar (*J. scopulorum*), dwarf juniper (*J. sibirica*), Colorado blue spruce (*Picea pungens*), Engelmann spruce (*P. engelmanni*), narrow leaf cottonwood (*Populus angustifolia*), Aspen (*P. aurea*), Rocky Mountain maple (*Acer glabrum*).

Such a complete merging of species whose habitats normally cover elevations varying from 5,000 to more than 11,000 feet is a very rare occurrence and may not be duplicated. It is certain to offer a very interesting field for scientific study.

The area is being made accessible through trail development, and other improvements will be added by the Forest Service to make it a novel field exhibit which will be set aside and protected for the benefit of the visitors to the National Forest.

A. C. NORD.

U. S. FOREST SERVICE,
OGDEN, UTAH.

SUSTAINING MEMBERSHIP FOR THE PUBLICATION OF LONGER CONTRIBUTIONS

The action of the Ecological Society of America, at its Nashville meetings, with reference to the publication of longer contributions will be reported in the proceedings of those meetings in the April issue of *ECOLOGY*, Volume IX, No. 2. Meanwhile, a preliminary note will be of interest to those who were unable to attend the Nashville meetings. The plan adopted involves the creation of a new class of membership, Sustaining Members, paying \$10.00 dues, of which \$6.00 will go toward the publication of longer ecological studies as supplements to the regular issues of *ECOLOGY*. The favorable reaction to this plan, and the large proportion of those present who agreed to transfer from Active to Sustaining Membership, are encouraging indications of the success of the plan. The following signed as Sustaining Members, one of them, already a Life Member, becoming a Sustaining Life Member by the payment of an additional \$100.00:

W. C. Allee, E. Lucy Braun, George P. Burns, Royal N. Chapman, R. E. Coker, Harold S. Colton, Henry C. Cowles, H. R. Eggleston, George D. Fuller, F. C. Gates, Ada R. Hall, Charles F. Hottes, Minna E. Jewell, Chancey Juday, L. A. Kenoyer, C. F. Korstian, Herman Kurz, Charles W. Lowe, H. F. McGinnis, Z. P. Metcalf, Robert C. Miller, Barrington Moore, G. E. Nichols, A. S. Pearse, Edwin B. Powers, M. C. Quillar, H. L. Shantz, Victor E. Shelford, Charles S. Spooner, E. N. Transeau, A. G. Vestal, A. E. Waller, W. G. Waterman, J. E. Weaver, A. O. Weese.

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THE QUANTITATIVE ANALYSIS OF ENVIRONMENTAL FACTORS¹

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Throughout the history of various branches of science there can be seen a trend from the field of relatively inexact pure description to the field of relative exactness involving quantitative methods and mathematical calculations. Progress has often been very rapid during the period of pure description and qualitative methods, but inevitably there has come a time when there has been a slowing of progress because the most outstanding observations have been made and recorded and because the perception of the human senses lacks the sensitiveness necessary to follow the more minute undiscovered details. This stage has later been followed by a great acceleration of progress when the quantitative methods have been introduced.

It was once believed that mathematical expressions must be confined to the description of surfaces and solids just as we now have a feeling that they must be confined to phenomena in the field of physics. It was once considered that heat conduction was subject to too many factors to permit itself to be handled by mathematical calculations, just as we now have a feeling that ecological phenomena are subject to so many factors that they do not lend themselves to mathematical methods. Those of us who are engaged in the study of animal ecology may do well to pause and consider the future of our branch of science in the light of the work of Fourier, who more than a century ago, began to apply mathematical methods to the study of the transmission of heat through solids. In this day when it is possible for physicists and engineers to calculate so exactly the amount of heat required to warm a given space surrounded by walls with given coefficients of conduction and subject to known external conditions, it is hard to realize that there was once a day when it seemed to be impossible to apply quantitative calculations to the transmission of heat. All of the objections which now stand in the

¹ Published with the approval of the Director as Paper No. 761 of the Journal series of the Minnesota Agricultural Experiment Station.

way of the use of these methods in ecology then stood in the way of the use of these methods in connection with thermodynamics.

As an illustration of the stimulus which is lent to science by the application of mathematical methods, we have Ohm following close upon Fourier in applying the methods of Fourier to the transmission of electricity through various conductors. He adopted the fundamental principles of Fourier, and was able to deduce the law which we know by his name and it has been changed only in details of the calculation of special cases. Here again there was an attempt to apply quantitative methods and mathematical calculations to a field which was little known and which seemed to contain so many factors that it would not lend itself to such exact methods. In the introduction to his original memoir Ohm said that its aim would be attained if, by means of it, the great variety of facts might be presented as unity to the mind. Again we ecologists may do well to pause and consider whether it would not be an advantage if it were possible, by a few principles, briefly stated, to make the great variety of facts, which are known in our branch of science, appear as unity to the mind. A consideration of the vast amount of purely descriptive material which is rapidly accumulating in the field of ecology will add to the appreciation of such a possibility.

The animal ecologists find themselves handicapped in the use of quantitative methods because of the difficulty in obtaining quantitative samples, the lack of a method of expressing the abundance of organisms, and of expressing the effect of the environment in terms of the quantity of organisms. As a result of the consideration of some of these handicaps, it has seemed that it might be possible to find some characteristics, essentially biotic, which could be used as a measure of the organisms and the environment, and which might be subject to experimental verification.

It has long been known that the possibilities of reproduction of the various species of organisms are enormous, and that they far exceed the realization which the species ever has in numbers of individuals. The fact that eventually but two out of an enormous number of progeny would survive to replace the parents, was an essential part of Darwin's theory of the survival of the fittest and the action of natural selection. Many calculations have been made to show the possibilities of the various organisms to reproduce.

Attention has been called to the possibilities of rapid reproduction in the protozoa by Woodruff ('22), Cutter et al. ('23), Myers ('27), in algae by Roach ('26), and for the vertebrates the information has recently been summed up by Elton ('27).

Woodruff stated that it was possible for a single infusorian to produce in sixty days time, a cubic meter of protoplasm with 1000 individuals to the cubic millimeter. In seven years time the progeny of this infusorian would be represented by a mass of protoplasm ten thousand times greater than the mass of the earth itself, and in a few hundred years it would exceed the whole visible universe including the sun and all the planets. We are in-

clined to look upon these calculations as amusing and possibly fictitious. Nevertheless it is a fact that *Drosophila* has made its great contribution to genetics because of its enormous reproductive potential which makes possible so many generations in such short periods of time. This high potential rate of reproduction is just as essential a characteristic of *Drosophila* as the high valence of Hydrogen is as a characteristic of that element.

Thompson ('23), Lotka ('25), Volterra ('26) and Pérès ('27), have considered the factors which enter into the stabilizing of populations. They have used mathematical calculations involving theoretical rates of reproduction, and have called attention to the mathematical laws involved in the expression of the trend of populations.

Pearl ('25) has experimented with cultures of *Drosophila* populations in environments of known size, and has concluded that populations of organisms usually follow rather definite trends and tend to approach the point of saturation for their environment. The variations in the abundance of insects, in so far as we have data to represent them, indicate a remarkable constance in numbers when compared with the potential number which might exist at any one time. Thus it seems that whatever the potential rate of development of an organism may be, its environment offers sufficient resistance to multiplication to cause its numbers to tend to remain constant. It is this fact, obvious though it may be, that will now be considered.

Let us return for a few minutes to an analogy drawn from Fourier's study of the transmission of heat through solid bodies. Fourier used the example of a metal ring of uniform consistency and cross section. When heat was continuously applied to one point on this ring, and external conditions remained constant, the temperature of the ring changed until it finally came into equilibrium, at which time the temperature was highest at the point where the heat was applied and lowest on the side of the ring opposite the point of application of the heat. When conditions remained constant and the heat continued to be applied to the ring, the temperature of the ring did not change at all. This, Fourier said, demonstrated that the rate of conduction of heat away from the ring was equal to the rate at which the heat was introduced into the ring. It was this case which attracted the attention of Ohm who cited an analogous case in which the electricity was conducted along a uniform rod from a positive to a negative pole. A state of equilibrium was attained in which the electric current was continually being introduced into the rod and yet the potential along the rod remained constant. From this he deduced the law that the measurable amount of current present at any one point at any time was equal to the potential electromotive force which was introduced into the rod, divided by the resistance of the rod. The great advantage in this expression was the fact that when two of the factors were known, for example, the measureable amount of current and the electromotive force which was introduced into the system, it was possible to calculate the value of the third factor—the resistance. This had to be an empirical unit.

and we know it, at the present time, as an "ohm," and it is important to note that an ohm is expressed in terms of the electric current itself. Thus it became possible to calculate the value for any one of the three variables when the other two were known. As a result of this, all of the various properties of elements and compounds which have to do with the conduction of electricity came to find their place in this simple empirical formula, and at the present time we have tables which give the physical constants of the various materials with respect to the conduction of electricity. Thus, what was formerly a multiplicity of insignificant detail was united into a simple but comprehensive expression of fundamental importance. All the essential facts may now be ascertained by consulting tables.

In drawing analogies from the works of Fourier and Ohm it is recognized that the cases may not be strictly comparable to animal abundance. Yet it seems evident that we have in nature a system in which the potential rate of reproduction of the animal is pitted against the resistance of the environment, and that the quantity of organisms which may be found is a result of the balance between the biotic potential, or the potential rate of reproduction, and the environmental resistance.

For this purpose, therefore, biotic potential may be defined as the mean maximum rate of reproduction in a given period of time under given conditions. The action of the environment, then, must necessarily be expressed in terms of resistance to this maximum rate of reproduction. An empirical formula similar to Ohm's formula, representing the concentration of organisms, or abundance of organisms, as equal to the biotic potential divided by the environmental resistance, may aid in making the complex factors of the organism and the environment appear as unity to us. At least, it is possible to conceive of everything as having a place in this formula. The environmental resistance will include the physical factors of the environment, temperature, humidity, etc. and also the biotic factors of the environment, parasites, competitors, etc. The advantage of the formula will be practically the same as those which Ohm realized. When concentration and biotic potential are known, a value may be ascribed to environmental resistance. A knowledge of any two of the three variables will make it possible to calculate the value of the third.

It is easy to postulate complicated conditions in which calculations might be difficult if not impossible. It is, however, more constructive to postulate simple conditions where calculations can be made and important conclusions arrived at.

The hypothesis needs the support of experimental data based upon controlled conditions. Such data have been obtained² from a study of the con-

² These experiments were planned, and preliminary determinations made, at the Rothamsted Experiment Station at Harpenden, England, and thanks are due Dr. A. D. Imms and Dr. R. A. Fisher for many suggestions and criticisms, and to Mr. E. A. Fisher of the British Flour Miller's Association Research Laboratory for preparing the

fused flour beetle, *Tribolium confusum*. This insect has the advantage of living in wheat flour which is a relatively stable environment. The temperature and moisture may be controlled easily. The size of the environment may be expressed in either grams or cubic centimeters. Large numbers of the beetles may be kept in a small space, and many generations may be had in a short period of time without the interruption of periodic dormancy. The female beetles lay continuously for several months (Chapman, '18) so that there is a great overlapping of generations. The period from egg to adult is roughly forty days at 27° C. The present series of experiments is concerned with the total populations of beetles, rather than with adults only, as will be explained later.

The conditions of the experiments were made as simple as possible. The object was to determine, first, whether a condition of equilibrium would be reached in which the population, as expressed in the number of individuals per gram of flour, would remain constant regardless of the size of the environment. Under such conditions the environmental resistance would be equal to the biotic potential and the conditions of the hypothetical formula would be satisfied. Secondly it was sought to determine whether the effective rate of reproduction of single pairs of beetles was inversely proportional to the environmental resistance, which, in this case, is a function of the total size of the environment.

To determine the first point, a series of environments was set up in which the depth of the pure whole wheat flour was constant at two centimeters, but the quantities of flour in the different environments formed a geometric series, containing 4, 8, 16, 32, 64 and 128 grams each. The populations of adult beetles which were introduced at the start also formed a geometric series such that there was one pair of beetles to each four grams of flour in each environment. The sexes of the beetles were determined but the ages were at random. The moisture was kept constant and the temperature was maintained at 27° C.

The eggs, larvae and pupae were counted and the flour renewed at each observation. The various stages of beetles were separated from the flour by means of standard silk bolting cloth (Chapman, '18). The numbers of the various stages of insects during the course of the experiments are shown in Table I. It can be seen that there was a rapid increase in numbers, which was followed by a condition of relative stability with practically no larvae or pupae. The number of eggs present at each observation is an indication of the total biotic potential of the population. In spite of the large number of eggs which were always present, there were no appreciable changes in the number of adult beetles. When eggs were removed from the culture they hatched on schedule time, and an equal number of new eggs appeared in the pure whole wheat flour. The major experiments were performed at the European Parasite Laboratory at Hyères, France. Dr. W. R. Thompson contributed materially to the work through his advice and criticism.

TABLE I. Total number of individuals in each environment. *Tribolium confusum* in whole wheat flour at 27° C. and uniform moisture.

Days	4 Grams				8 Grams				16 Grams				32 Grams				64 Grams				128 Grams			
	Eggs	Larvae	Pupae	Adults	Eggs	Larvae	Pupae	Adults	Eggs	Larvae	Pupae	Adults	Eggs	Larvae	Pupae	Adults	Eggs	Larvae	Pupae	Adults	Eggs	Larvae	Pupae	Adults
0																								
15	41	17	0	2	62	71	0	4	127	187	0	8	263	280	0	16	631	686	0	32	854	1543	0	64
30	44	74	0	2	30	168	0	3	103	314	0	8	188	509	0	16	369	1118	2	32	393	2371	99	61
50	42	45	21	31	47	75	51	90	89	178	79	167	383	310	114	332	402	792	220	639	1265	1204	503	1405
64	64	20	14	59	107	47	12	144	205	78	36	220	497	180	58	414	1145	400	157	842	2215	541	198	1832
78	60	10	6	65	114	11	20	144	330	16	39	158	636	14	91	428	1254	67	159	875	2705	230	256	1857
101	89	5	1	66	185	30	0	156	390	46	1	174	861	94	3	445	2086	146	1	928	2672	318	2	1906
114	125	2	0	66	180	20	7	156	368	21	13	174	846	56	20	449	1530	97	16	904	2943	218	48	1914
134	81	0	0	66	257	3	0	159	460	24	1	174	842	13	0	452	2143	32	4	908	3805	63	4	1905
156	89	0	0	65	236	2	0	157	544	8	9	173	837	6	4	445	1912	45	7	902	4097	63	10	1882

original culture. This demonstrates the fertility of the eggs. The fact that the lack of increase in the population was due to the eggs being eaten by the adults was demonstrated by placing eggs in cultures which contained only male beetles. The per cent of eggs eaten varied directly with the population of adults per gram of flour. Pupae, and to some extent larvae, were also eaten in environments which contained high concentration of beetles. Thus we have an environmental resistance which is a function of the size of the environment.

The number of individuals per gram of flour oscillated about a constant, and was practically the same for each environment, as may be seen in Table II. This is further demonstrated by Table III which presents the results of a series of environments of the same size which were started with 1, 2, 4, 8, 16 and 32 pairs of beetles each, and which came to equilibrium at about the same number of individuals per environment. Small original populations saturated the environments in short periods of time, producing populations equal to those in environments which started with many times the same original populations. Tables II and III show the number of beetles per gram of flour, and indicate that the populations attained equilibrium in about eighty days. Tables I and II are based upon the same data, the former giving the total number of individuals in each environment, while the latter gives the number of individuals per gram of flour in the same environments. Attention is called to the fact that an accident occurred to the 16 gram environment which resulted in a reduction from 220 adults on the 64th day to 158 on the 78th days, as may be seen in Table I.

TABLE II. *Beetles (Tribolium confusum) per gram of flour*

Days	4 G.	8 G.	16 G.	32 G.	64 G.	128 G.
	5	.5	.5	.5	.5	.5
15	15	17	20	17	21	19
30	30	25	26	22	24	23
50	35	33	32	35	32	34
64	39	39	34	39	40	37
78	35	41	39	36	37	39
101	40	46	38	44	49	39
114	48	45	36	43	40	40
134	37	50	41	41	48	45
156	38	49	46	44	45	47
171	46	49	46	43	42	40

The mean number of individuals per gram of flour in all of the environments after the attainment of equilibrium was 43.97 with a standard deviation of 4.27 and a probable error of 2.88. No personal selection of data was exercised. A regression line was calculated from the first series of experiments, and data from all other experiments compared with this line. When the number of individuals per gram of flour fell within a zone represented by

the standard deviation of this regression line, all of the data from the experiments under consideration were arbitrarily used from that day on. Consequently the mean value of 43.97 with a probable error of 2.88 represents the facts of the case, and any judgment as to the validity of the conclusions to be drawn must be based upon this result.

TABLE III. *Beetles (Tribolium confusum) per gram of flour*

Days	32 G.	32 G.	32 G.	32 G.	32 G.	32 G.
	.062	.125	.25	.5	1	2
11	1.15	5.5	9	16	27	42
25	2.5	12	19	20	30	38
54	11	27	32	30	43	55
69	28	31	30	29	46	47
81	30	44	42	43	53	53
104	40	43	38	42	52	44
123	45	43	39	50	50	46
139	42	47	42	44	50	45

The first point, therefore, seems well demonstrated. A condition of equilibrium is attained in which the biotic potential is equaled by the environmental resistance and the population remains relatively constant.

TABLE IV. *Beetles (Tribolium confusum) per gram of flour*

Days	4 G.	8 G.	16 G.	32 G.	64 G.	128 G.
	.5	.25	.125	.0625	.031	.015
8	14	6.8	1.7	1.46	.04	.04
28	32	19	14	6	3.3	1.67
41	33	24	15	8	5	2
63	36	31	34	24	18	13
79	43	44	35	28	20	23
97	52	46	42	35	28	23
117	41.5	38	38	28	25	29
135	41	40	44	37	30	28
154	44	44	40	32	24	31

For the second point, namely the relation between the increase of a population and the size of the environment, attention is called to Fig. 1. In this series of experiments a single pair of newly emerged adult beetles was placed in each of the environments which formed the same geometric series of sizes as in Table I. In this case, in the same period of time, one pair of beetles gave rise to 178 individuals in an environment of 4 grams and another gave rise to over 4,500 in 128 grams. The intermediate environments had populations of intermediate sizes. The numbers of beetles per gram of flour are shown in Table IV, and it will be seen that the smaller environments have reached a state of equilibrium and that this point falls within the limits set by Tables II and III. The larger environments have not yet come to stability, but they seem to be following about the same course as was fol-

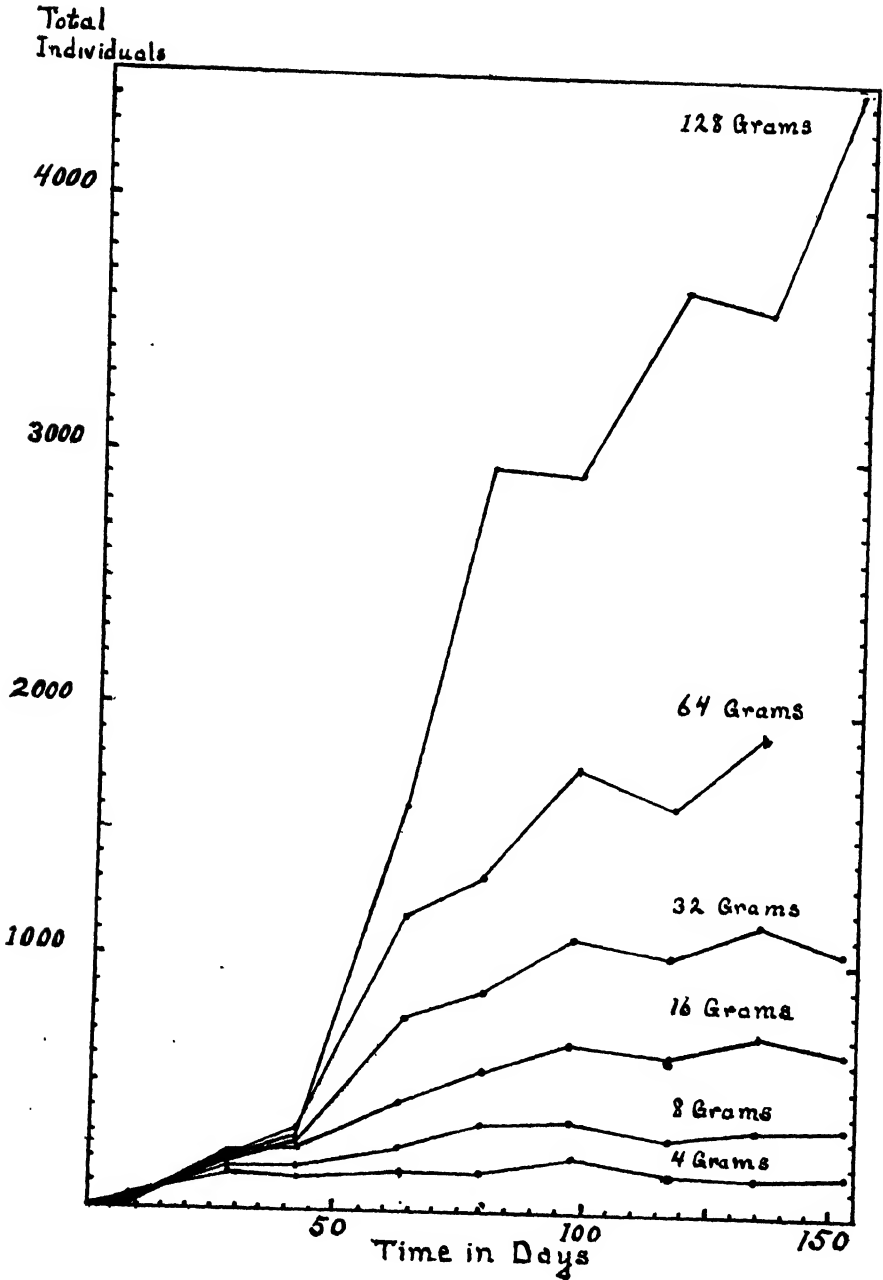


FIG. 1. Graphs showing increase in number of individuals of the confused flour beetle (*Tribolium confusum*) in different quantities of whole wheat flour at 27° C. and uniform moisture.

lowed by the smaller ones. During the first 40 days the total increase in numbers was about the same in all environments, although some resistance appeared in the smaller environments. After the first 40 days the daughters of the original females began to reproduce and the larger environments very rapidly exceeded the smaller ones. In this series of experiments all of the idiosyncrasies due to starting with single females chosen at random are present, yet the results are quite constant.

The second point seems, therefore, to be proven, namely that the increase of a population is proportional to the total size of the environments and, therefore, inversely proportional to the environmental resistance.

These results substantiate the hypothesis regarding the relationship between biotic potential, environmental resistance and insect abundance. The systems seem quite comparable to the physical systems studied by Ohm and Fourier. A high potential is ever present, and when the environmental resistance is lowered by the death of adults, eggs hatch and produce new adults to take the place of those which have died. The system is thus somewhat analogous to one with a host and parasite with perfectly synchronized life cycles.

The present discussion is based upon the total population including eggs, larvae, pupae and adults. If adult beetles only are considered the situation is more complicated and will be considered in a subsequent publication. It can be seen from Table I that the numbers of adult beetles form a geometric series similar to that of the total population, particularly in the larger environments. However, in the 16 gram environment the number of adults was reduced by accident on the 78th day and the number of adult beetles did not return to the former number which was in line with the geometric series. The total number of eggs, larvae and pupae increased to such an extent that the total population was in line with the series. The complicating factor of competition between adults and larvae must be postponed for the present.

It is rather obvious that the formula $C = Bp/R$ must hold when C is the concentration of insects, Bp the biotic potential, and R the resistance. When we substitute the known values and solve for the value of resistance we get $43.97 = \frac{(43.97 \times 8.4) .25}{R}$ or $R = \frac{(43.97 \times 8.4) .25}{43.97}$. The average num-

ber of eggs laid per female per day is 8.4 for these experiments, and 25 per cent of the population are females. The obvious solution is that $R = 2.1$. This is naturally the formula expressing the state of equilibrium and not the original increase of the population. Time does not enter into the formula in this case because population does not change with time.

The mere substantiation of the hypothesis would be of little consequence if it were not that by means of the method the quantitative analysis of environmental relationship is made possible. The valuation of each factor becomes subject to experimental verification. It is only necessary to vary one

factor at a time and determine its effect upon the potential and actual populations.

At first the total value of environmental resistance is unassignable to definite factors. But, as the value of each factor is determined, a distinction can be made between the value which may be assigned to definite factors and the value for the unknown factors. As investigations proceed, the known portion of the environmental resistance will become larger and the unknown smaller until the day may come when the unknown portion is small enough to be neglected for practical purposes.

Thus, in the study of this particular species, the way seems open for the logical and methodical analysis of the environmental relationships. In the course of such an investigation certain fundamental principles are to be demonstrated which apply to animals in general, many of which do not lend themselves to such close analysis.

The next logical step is the consideration of the potential and resistance represented in each species of a natural community of organisms which are interdependent and self supporting. The analysis of such a system is complex but the analysis of the tensions and phases of a physical system is also complex but nevertheless possible.

That objections will be raised to the use of laboratory results for field conditions, may be predicted on the basis of past experience. In answer to such objections it is sufficient to say that there is no surer way to progress than by the comparison of the results from careful determinations and calculations under known conditions with those which are to be found in the field. If the theoretical predictions account for nearly 100 per cent of what is found in the field, we may consider the problem as solved for all practical purposes. If there is a wider difference, which is probable, our search for the unknown may be guided by a logical process of elimination and more minute analysis. The history of the physical sciences offers abundant support for such procedure. By following this precedent, ecology may become one of the more exact of the biological sciences.

SUMMARY

The hypothesis assumes that the balance of numbers of organisms in nature is maintained by the tendency of the organisms to produce large numbers of offspring and for the environment to take a large toll from the numbers produced. This balance of the potential rate of reproduction and the resistance of the environment, which results in a relatively constant number of organisms, seems comparable to such physical phenomena as the reduction of an electric current by the resistance of the system through which it passes, which results in the current being equal to the potential current divided by the resistance of the system. The hypothesis is tested by a series of experiments under controlled conditions in which flour beetles (*Tribolium confusum*) are maintained in environments of known size. It was found that the numbers

of individual's increased until there were 43.97 per gram of flour. Even though thousands of eggs were laid daily the numbers of individuals remained constant at 43.97 with a standard deviation of 4.27 and a probable error of 2.88. Since it was shown that the adult beetles ate the immature stages in proportion to the concentration of individuals per gram of flour, the hypothesis seems to be substantiated. It is suggested that environmental factors may be measured in terms of their effect in reducing the potential rate of increase. Thus all factors may be measured on the same scale and their values compared directly.

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A RECORDING ATMOMETER ¹

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The methods of obtaining continuous records of the loss of water from atmometers are not satisfactory, and usually require hourly weighings or readings. This requires too much work especially if records over a long period of time or under field conditions are required. The automatic recording balance described by Transeau ('11) is satisfactory under laboratory or greenhouse conditions; but it cannot be used in the field because the apparatus is very easily disturbed by slight air currents. A recording atmometer similar

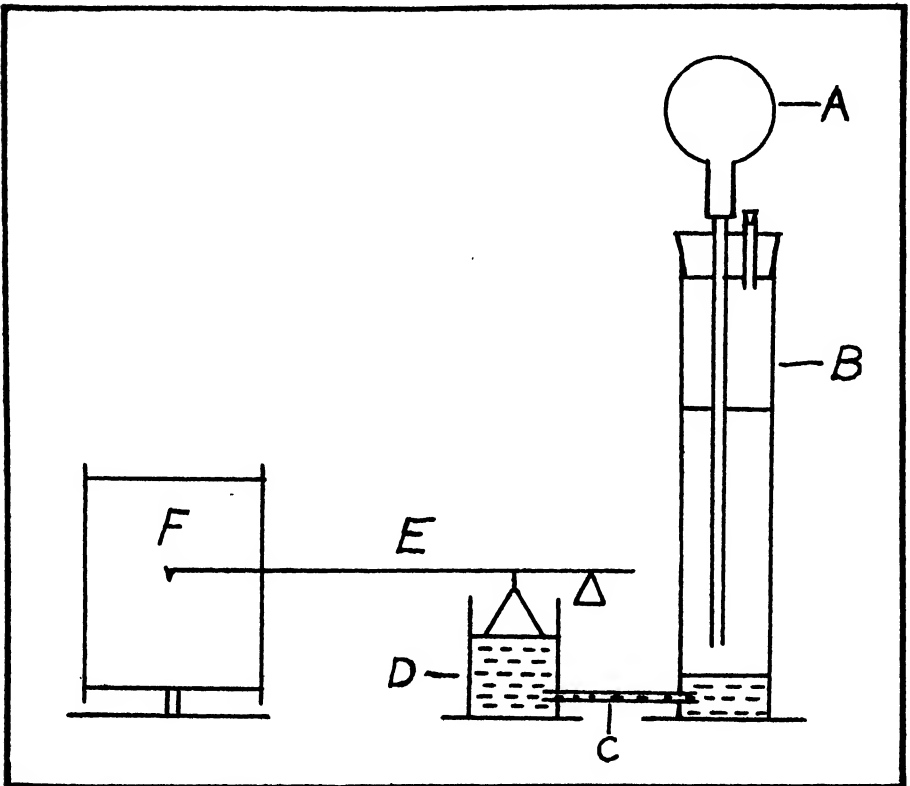


FIG. 1. Diagrammatic sketch of the recording atmometer.

to the instruments used in obtaining continuous records of temperature and humidity is needed for such work.

¹ Papers from the Dept. of Botany, Ohio State University No. 211.

Undoubtedly many people who have measured evaporation in their work have tried to devise instruments for automatically recording it. However, there are few successful instruments of this kind in use. Allee ('26) used a recording evaporimeter made by Jules Richard in France for ecological studies in Panama. He published record sheets of the evaporation rates obtained with this instrument, but states that he had some trouble with the instrument. Briggs and Shantz ('15) used an open pan evaporimeter, and recorded the loss in weight with an automatic balance. Livingston and his students have devised several recording atmometers. No attempt is made to report all recording evaporimeters which have been made. As far as is known the one sold by Jules Richards is the only one on the market.

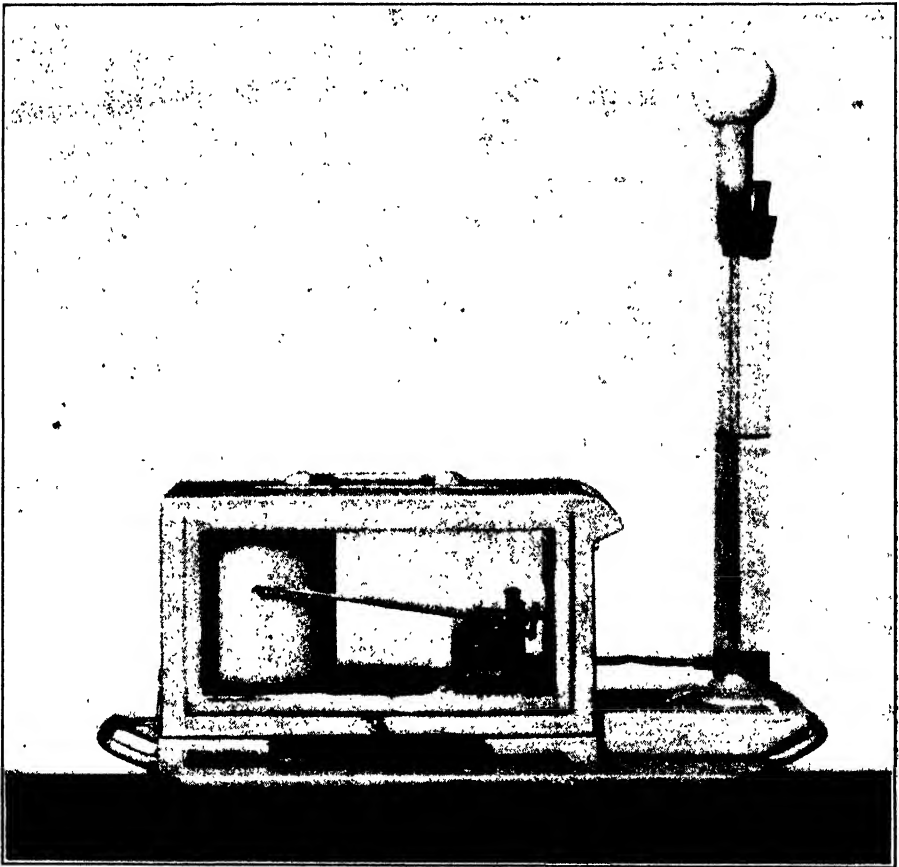


FIG. 2. The recording atmometer.

The principle of the instrument described here and used with considerable success during the summer of 1927 is quite simple and somewhat different from any other instrument described before. Figure 1 is a diagrammatic

sketch of the principle of the instrument. *B* is a tall cylinder of uniform diameter. It is connected with *D*, a low cylinder of similar diameter, by a glass tube *C*, through holes very near the bottom. When mercury is placed in the cylinders it becomes level in both arms. If water is now placed in *B* the level of the mercury in *D* is raised. As water is taken up through the tube and lost by evaporation from the atmometer sphere *A*, the level of the mercury in *D* falls. This change in level of the mercury in *D* is recorded on a drum by means of a float, lever arm, and a pen.

The instrument is calibrated by adjusting the lengths of the lever arms which carry the float and the pen, and the amount of the mercury in the cylinders. This adjustment is made so that a loss of a certain number of cubic centimeters of water is a uniform interval across the record sheet. The number of cubic centimeters of water corresponding to the smallest division on the record sheet can then be easily found. Or the adjustment may be made adjusted so that a single division is equal to a certain number of cubic centimeters of water loss from the atmometer. In the instrument as used in our experiments the smallest interval on the chart is equal to 4 cubic centimeters of water. This instrument held about 200 c.c. of water, and was large enough to run for a week under the conditions where it was used. The sensitivity of the instrument can be varied by changing the diameter of the cylinders. Figure 2 shows the instrument. Total amounts of water evaporated during the 24 hour day, or a week can be obtained from this instrument as well as the rates per hour. It is not necessary to describe the method of calculating these values since it is quite obvious to anyone doing this kind of work.

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THE RÔLE OF MICROORGANISMS IN THE TRANSFORMATION OF ORGANIC MATTER IN FOREST SOILS

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According to Ramann, one of the earliest students of forest soils, the biology of the soil comprises all the changes that take place there under the influence of organic life. A study of the microbiological processes in the soil should, therefore, comprise not only the determination of the microscopic population but also of the various transformations brought about by numerous members of this population in the soil. The chemical changes thus brought about in the organic and the inorganic constituents of the soil giving rise to the so-called "forest humus" represent rather difficult problems in organic chemistry; this is largely the reason why so little progress has been made in our understanding of the nature of the biological processes in forest soils and their rôle in the nutrition of higher plants.

A large number of the investigations dealing with the functions of microorganisms in forest soils can be grouped around the transformation of nitrogen. Even the soil organic matter or "humus," commonly spoken of as either "raw humus" or as "mull" depending upon the conditions of its formation, has been considered only as far as it formed a source of available nitrogen in the soil; among the products of decomposition of this organic matter ammonia and nitrate have usually been determined, the latter being produced only under certain conditions. The numerous other soil processes attracted no attention at all or have been considered only in a very general way. The nature of the fixation of nitrogen in forest soils, for example, has remained very vague, since neither *Azotobacter* (Weis and Bornebusch '17) nor legume bacteria are found to occur to any extent in these soils, especially in the "raw humus" soils. The transformation of the non-nitrogenous complexes of the soil organic matter, if investigated at all, has been limited to a study of the liberation of carbon dioxide, which is evidently essential for tree growth. The decomposition of celluloses, hemicelluloses including pentosans, lignins, resins, tannins, and the various other non-nitrogenous constituents of the forest plant residues attracted only little attention. Whatever is known of these processes in forest soils has resulted either from the investigations by plant pathologists on the activities of parasitic and semi-parasitic fungi (Hartig '78, Ward '98), or from the work of wood technologists on the decomposition of wood by pure and mixed cultures of fungi, or by the interpretation of bacteriological and other microbiological processes in field and garden soils.

It is only within the most recent years that the subject of decomposition of the various constituents of the natural organic materials added constantly to the soil in the form of leaves and other tree products as well as shrubs, mosses and the rest of the forest vegetation, has been receiving some attention and an attempt has even been made to learn the nature of the organic complexes which go to make up the forest "humus." Koning ('04) came to the conclusion that the hyphomycetes probably play a much more important rôle than the bacteria in the process of "humification" in forest soils, or the transformation of the forest leaves into "humus." The organic residues were found to possess a characteristic fungus flora at the different stages of decomposition, the distribution of the fungus spores through the soil being carried out actively by the flies, mites and larvae. Leaves of *Quercus* were much richer in fungi than leaves of *Fagus* and needles of *Pinus*, since the former offer more readily available nutrients to the microorganisms. The forest "humus" itself could be used by ordinary filamentous soil fungi, such as *Trichoderma koningi*, only as a source of nitrogen but not of carbon. Actinomyces were not found to any extent in forest soils and were not believed to take any active part in the decomposition processes. Hartig ('78) and von Schrenk ('00) have shown long ago that different types of fungi are concerned in the decomposition of celluloses and of lignins in wood materials. Even the same kind of wood was found to be acted upon in a different manner by different fungi. *Polyporus juniperinus* growing on *Juniperus virginiana* attacked the lignins largely, and reduced the wood fiber to almost pure cellulose; *Polyporus carneus* growing on the same wood decomposed the cellulose almost entirely. Falck ('26, '27) suggested the terms *destruction* and *corrosion* for the two processes of decomposition. In destruction, the celluloses are rapidly decomposed while the lignins are largely left intact; the genera *Merulius*, *Coniophora*, *Poria*, *Lenzites*, etc. are primarily concerned in this process. In corrosion, the lignins are attacked while the cellulose fibers are spared; *Polyporus annosus* Fr. (*Trametes radiciperda* Hartig) is a typical form bringing about this process. Pentosans are attacked in both cases, although some of them may persist as long and even longer than the celluloses. These activities, namely the decomposition of wood products, are carried out largely by various filamentous fungi and Hymenomycetes. The presence of saprophytic bacteria may increase materially the rate of decomposition by fungi (Schmitz, '19); cellulose-decomposing bacteria do not seem to play any important part in the decomposition of wood under natural conditions (in the so-called processes of decay).

According to Rege ('27) natural organic materials including wood products contain two types of furfural-yielding constituents, some of which are even more readily decomposed than the celluloses, while others are more resistant to decomposition. Whether the more rapid complete disappearance of the celluloses than of the hemi-celluloses (although in the beginning of decomposition the pentosans are attacked more rapidly than the celluloses)

is due to this cause, as was also found by Bray and Andrews ('24), or whether this is due to the formation of hemi-celluloses by the microorganisms, as believed by Rose and Lisse ('17) and others, still remains to be seen.

The nitrogenous complexes of forest soils originate from plants and, probably even to a much larger extent, from the mycelium of the so-called humifying fungi. These complexes are modified proteins, otherwise most of the nitrogen in the humus should be isolated from the soil in the form of proteins or their derivatives. According to Süchting ('25), the nitrogen compounds in forest soils are largely heterocyclic in nature, such as derivatives of pyridin and its higher homologues.

The forest and its soil are in harmonious equilibrium. Almost eighty per cent of the nutrients assimilated yearly by the trees goes back to the soil in the form of leaves, needles, twigs, fruits and other tree products; only about 20 per cent is retained by the tree itself. This 80 per cent of nutrients becomes again available to the trees only after a period of decomposition, which may last from one to many years. If these organic residues are not decomposed very rapidly, the tree must obtain from the soil not only the 20 per cent necessary for its own annual structural needs, but also the 80 per cent which it returns later to the soil in a combined organic form. Süchting considered, therefore, the forest in which the organic residues decompose in one to three summers, as having healthy soils containing sufficient nutrients, especially calcium. In those cases where rapid decomposition does not take place, but where the organic residues are changed largely into "humus," nutrient-poor soils result, with very unfavorable water relations. This accumulation of organic matter leads to a more and more limited amount of nutrients available to the growing trees, which diminish constantly in growth. The formation of "humus" in soil is thus to be looked upon as a very injurious factor in tree growth. Once "humus" formation has set in, it proceeds very rapidly, so that a layer of organic matter, 10 to 30 centimeters deep, accumulates in 50 to 70 years, while the various tree residues added yearly to the soil hardly undergo decomposition.

To understand these processes of decomposition, it is quite essential to have a clearer concept of the microbiological population and the processes that the various representatives of this population bring about in forest soils as well as the environmental conditions modifying the nature of this population and its activities.

The forest flora consists predominantly of fungi, among which the Basidiomycetes play not the least important rôle. The earlier students of forest soils (Müller, Ramann) recognized this fact and were even inclined to consider these organisms as the only agents in the microbial transformations in those soils. This is well brought out in a determination of the relative abundance of fungi and bacteria by the plate method; the results thus obtained represent, however, only a very low minimum as far as the fungi are concerned. In normal field and garden soils bacteria predominate

both in numbers and in the variety of activities, while in forest soils the fungi are much more abundant, especially when the actual amount of microbial cell substance is computed. Ramann *et al* ('99) reported that the numbers of bacteria per gram of organic matter in various forest soils range from 2,050,000 to 59,880,000 and the numbers of filamentous fungi from 66,000 to 10,280,000 per gram (and even more). This number of fungi represents only the spores found in a given quantity of soil. The plate method gives no information at all concerning the great mass of fungus mycelium, especially of the Basidiomycetes, which permeates all the organic matter in forest soils. Students were, therefore, warned not to rely upon the plate count of fungi. It was suggested that the abundance of mycelium be determined by making a microscopic examination of the soil which reveals the organic matter as a mass of hyphae holding together some of the plant residues. Falck ('23) has even gone a step further and attempted to differentiate the various types of forest soil on the basis of the active microflora and microfauna and the processes of transformation of organic matter brought about; the nature of the flora and fauna depend of course upon the soil and the environmental conditions. Certainly so far as the initial stages of decomposition of organic matter in forest soils are concerned, the fungi were found to be by far more active than the bacteria.

Similar results were reported by Bokor ('26), namely that forest soils contain smaller numbers of bacteria than field and garden soils, especially those receiving stable manures. The reaction of the soil, as expressed by the pH, controls the number of bacteria in the soil as found by the plate method: with a constant pH, the numbers increase with an increase in the content of organic matter and air capacity; nitrogen-fixing bacteria in forest soils can withstand a higher acidity than in agricultural soils; soils of mixed forests contain more bacteria than soils of deciduous forests, and these more than soils of coniferous forests, although, from the relation of bacteria to pH, one would expect that forests of mixed coniferous and deciduous species, since they are generally more acid than deciduous forests, would have less; various anaerobic bacteria, especially the butyric acid bacteria, are found abundantly in forest soils, while the number of nitrifying bacteria is very low.

Attention should also be called to the results of Düggele ('23), who made a study of the numbers of different types of bacteria (using the plate and dilution methods) in a series of soils from 10 evergreen and 9 deciduous forests. The numbers of bacteria growing on the gelatin plate were found to range in the former from 225,000 to 2,270,000 and in the latter from 370,000 to 6,700,000 per gram of soil, the numbers increasing with an increase in the lime and in the organic matter content of the soil. The relative abundance of the bacteria developing upon the agar plate was found to be quite similar. The total numbers of anaerobic bacteria, as determined by the shake tube method, were found to be between 50,000 to 300,000 in the

evergreen and from 70,000 to 400,000 in the deciduous forest soils. Among the specific anaerobic bacteria the following numbers were reported per gram of soil: about 100 cells of denitrifying bacteria, 100 to 10,000 proteolytic bacteria, 100 to 100,000 butyric acid bacteria, 100 to 10,000 anaerobic nitrogen fixing bacteria and a few single cells of anaerobic cellulose decomposing bacteria (from none at all to 2 cells per gram of soil). Practically all the soils contained urea-decomposing and pectin decomposing bacteria, in numbers of 1,000 to 100,000 per gram. Aerobic nitrogen fixing bacteria were found only in 4 out of the 19 soils, in quantities ranging from 0.2 to 200 cells per gram, while nitrifying bacteria were found in only 3 out of the 19 soils (2 to 100 cells per gram), both groups, namely the aerobic nitrogen-fixing and the nitrifying bacteria, occurring only in soils having a neutral reaction, but not in the acid soils. In general the largest number and greatest variety of bacteria were found in the neutral soils.

According to Bokor ('27) both aerobic and anaerobic cellulose decomposing bacteria are found in forest soils even at a pH of 4.3. The large number of anaerobic bacteria in forest soils (from 500,000 to 5,000,000 per gram of soil) should attract particular attention; the same is true of the anaerobic nitrogen fixing bacteria (100 to 10,000 per gram). The fact that the aerobic nitrogen fixing bacteria are either entirely lacking in forest soils or are present there only to a very limited extent, points definitely to the rôle of the anaerobic organisms in the fixation of nitrogen in these soils.

As pointed out above, the transformation of organic matter in forest soils has been considered largely from the point of view of nitrogen transformation. The nitrogen content of forest "humus" usually ranges from 1.5 to 3.0 (extremes 0.6 to 4.3) per cent (Hesselmann, '26). The higher the pH value of the organic matter the higher is its nitrogen content. In the decomposition processes taking place in "raw humus" soil, the nitrogen is liberated as ammonia, while in the so-called "mull" soils, the ammonia is rapidly changed to nitrate (Gaarder and Hagem, '19, '20). The decomposition processes depend on the reaction of the soil, buffer content, nature of nitrogen complexes, moisture, climate, temperature, etc. The optimum pH for ammonia formation was found to be 4.5 to 5.0, for nitrate formation, in case the soil is inoculated, pH 5.5 to 6.0, and nitrate formation in uninoculated soil pH above 6.0.

Boussingault ('86) was the first to establish the presence and formation of nitrates in forest soils; in spite of that, however, the voluminous literature on the subject remained very confusing. It was commonly assumed that, though field and garden soils produce nitrates abundantly, there is very little nitrate formed in forest soils, if any (Ramann, '20). Weis ('10) demonstrated that nitrates are formed in all sorts of forest soils, but in varying amounts. Nitrification takes place not only in the warm summer months but also in the autumn. The so-called "mull-types" of forest soils contain considerable quantities of nitrate while the "raw humus" soils contain only

traces of assimilable nitrogen but considerable quantities of combined nitrogen; the latter can readily be made to change into nitrate by liming and cultivation of the soil.

According to Hesselmann ('26, '27) and others, the formation of nitrates in forest soils is an important ecological factor which considerably influences the type of plant association. Hesselmann divides all forest soils into nitrifying and non-nitrifying, the former comprising the birch, oak and other forest soils in which the organic matter is well intermixed with the mineral materials, while the latter comprise the evergreen soils rich in mosses and lichens in which the organic matter is largely "raw humus" and dry peat; the first are brown soils, the second podsol soils. Although the process of nitrification is not an essential factor, it is a favorable condition in the regeneration of forests. Melin ('27) has further shown that an active liberation of nitrogen, especially in the nitrate form, or a factor closely connected with it, favors an optimum development of mycorrhiza and is of great importance in establishing the equilibrium between the two symbionts. Active nitrification takes place in forest soil even at pH of 3.9-4.1. In soil layers exposed to light, nitrification takes place actively; in shady forests, ammonia formation takes place under thin cover, but little nitrogen is liberated under the thick cover of "raw humus." One may, therefore, justify the general conclusion that the nature of forest vegetation and tree growth depends upon the transformation of nitrogen in the soil, and in turn largely affects the nitrogen conditions.

In respect to ammonia formation in forest soils, definite results have been submitted (Clarke, '24, Kvapil and Nemec, '25) that the more acid the soil is the more ammonia there is formed. Aaltonen ('26) expressed his doubts whether nitrification plays such a predominant rôle in the regeneration of forests. His results point to the fact that large quantities of ammonia are formed in forest soils and that trees in ordinary moss forests do not receive the nitrogen in the form of nitrate. He agreed, however, with Hesselmann that forest soils can be classified into nitrifying (grass-herb forests) and non-nitrifying (moss forests). The better the forest type the higher is the nitrogen content of the soil and the larger is the amount of nitrogen in a mineralized form (ammonia and nitrate nitrogen). Nemec ('17) found that the resin content of the organic matter and the acidity of the soil are important factors both in the formation of humus in the surface layer of forest soils and in the rate of nitrification, these processes varying inversely with the amount of resins present and the degree of acidity.

Next to the rôle of available soil nitrogen in controlling the growth of forest trees, the evolution of carbon dioxide which is essential for the photosynthetic processes has received considerable attention (see summary by Romell, '22). According to Fehér ('27), the reaction of forest soil, by modifying the numbers and activities of microorganisms, influences the carbon dioxide evolution, the largest amount of CO_2 being produced in soils con-

taining the largest number of bacteria. High numbers of bacteria may not always correspond to an intensive evolution of CO_2 , as in the case of a swampy alder forest, due to the predominance of anaerobic bacteria. A sandy soil may show a relatively high evolution of CO_2 and a low number of bacteria, due to intensive activities of these under favorable conditions. The number of aerobic cellulose decomposing bacteria, however, was found to be parallel with the evolution of CO_2 .

This information concerning the nature and transformation of organic matter in forest soils is far from sufficient to afford us a complete picture of the rôle of microorganisms in these transformations. By far the most important problem in this connection, namely the nature of the "humus" which is formed from the plant residues making the forest soil what it is, a storehouse of all the nutrients that the tree requires for its growth, remains as much of a puzzle now as it ever was. Except for a few isolated studies and numerous speculations concerning its nature and origin, this "humus," as much as soil or peat "humus," still remains largely a matter of speculation.

Usually no attempt has been made to differentiate between plant residues undecomposed or in the process of decomposition, on the one hand, and the residual organic matter formed as a result of decomposition of the plant constituents by microorganisms under favorable conditions, on the other. Hesselman was among the very few to make such a differentiation. He suggested the term "Förna" for the unchanged plant and animal residues; "Förmalningsskiktet" or "Vermoderungsschicht," for the layer of humus consisting largely of the plant residues undergoing decomposition (F layer); "Humussäumneskiktet" or "Humusstoffschicht" for the layer of humus which consists of newly formed amorphous organic substances, in which the structure is no longer discernible (H layer).

The results obtained in the study of decomposition of organic matter in field soils can be utilized in interpreting some of the decomposition processes in forest soils. However, the forest soils present certain specific problems, both in the nature of the organic matter, in the conditions under which the decomposition processes take place, and in the nature of the microorganisms active in these processes, all of which make the "humus" in these soils quite distinct from that in cultivated, prairie and peat soils. Whether we accept the ideas prevalent until the middle of the last century concerning the rôle of "humus" in plant nutrition or the mineral theory of von Liebig which supplanted the "humus" theory, one thing is certain, namely, that we must understand the nature of this "humus" if we want to learn the mechanism of transformation of nutrients in the soil, whereby the carbon, nitrogen, phosphorus, and other elements assimilated by the tree, either through its leaves or through its roots, from the atmosphere or from the soil, are again made available for plant growth.

The organic matter added constantly to the soil in the form of plant residues consists predominantly of non-nitrogenous substances (sugars,

starches, pectins, pentosans, celluloses, cutins, lignins, oils, fats, waxes, resins, etc.). Most of these substances are sooner or later decomposed, thereby serving as excellent sources of energy for the numerous fungi and bacteria bringing about the decomposition processes. This energy enables the organisms to synthesize considerable cell substance. Some of the microorganisms are very efficient in the energy utilization, building up as much as 30 to 40 parts of organic matter (on a dry basis) for every 100 parts of plant material decomposed. To be able to synthesize this extensive mass consisting of mycelium, spores, bacterial and protozoan cells, the cell substance of the numerous worms, insect larvae, etc., considerable quantities of nitrogen, phosphorus and smaller quantities of other minerals are required. The amount of nitrogen in the forest products is very limited, being not more than 0.5 to 1.0 per cent in the mature materials; the nitrogen content of microbial protoplasm is, however, 3 to 10 per cent. In view of the large amount of the cell substance synthesized in respect to the plant products decomposed, the available nitrogen will be a limiting factor in the early stages of decomposition of the plant materials, and the tendency will be for most of the nitrogen to be stored up in the form of microbial cell substance. The unfavorable action of wood and wood products upon plant growth was finally shown (Söderbaum and Barthel, '24, Viljoen and Fred, '24) to be due to the assimilation of available nitrogen by microorganisms which use the celluloses and other carbohydrates of the plant constituents as sources of energy. The addition of available nitrogen, such as nitrate, tended to reduce the inhibitory effect of wood products.

The nitrogen stored away in the microbial cells is not readily available for plant growth unless it is at first decomposed by various bacteria or by other fungi. Falck ('23) has shown, for example, that while the roots of flax, oats and peas are unable to use the nutrients stored up in the fungus mycelium, young pine trees can do so quite readily; furthermore, this source of nutrients is excellent for the development of the pine trees, due probably to association of these trees with mycorrhiza fungi. According to Süchting ('25), the unavailability of the organic matter in forest soil ("raw humus") for plant growth is not due to any toxic action of the "humus" but to a lack of available nitrogen, since the nitrogen complexes in the "humus" are decomposed only very slowly. He also suggested that mycorrhiza are probably capable of breaking up these complexes. The increase in alkali soluble constituents, and the greater reduction of cellulose than of total organic matter decomposed which has been observed in the decay of wood by chemists and pathologists, both in the "white rots" (more rapid disappearance of lignins), and in the "brown rots" (more rapid decomposition of celluloses (Bray, '24, Bray and Andrews, '24)), is due to the synthesis of microbial cell substance (Waksman, '27).

As a result of his studies on the decomposition of organic matter in

forest soils, Falck ('23) differentiated two groups of processes which he terms as *mycocriny* and *anthracriny*.

Mycocriny comprises the decomposition of plant products exclusively by fungi; a definite flora of wood-destroying fungi (Basidiomycetes), accompanied by various molds and myxomycetes, can bring about the complete destruction of the plant residues. The total carbon is changed partly to CO_2 and is partly used for the synthesis of the fungus mycelium, while the nitrogen and minerals of the plant products are largely changed into fungus mycelium and spores. The synthesized mycelium and spores are an excellent forest fertilizer, and form the "acid humus" or "raw-humus" soil.

In anthracriny the process of decomposition of forest products by fungi is interrupted by various soil insects, larvae and worms that consume the mixture of plant residues which has been previously thoroughly attacked by the fungi and the fungus mycelium itself; these animals excrete later dark, "humus"-like residues. This material can now undergo the process of nitrification, and the soil thus formed belongs to the "mull" type.

An attempt will be made to present in this paper a series of data dealing with the processes of formation and decomposition of the organic matter in forest soils which will tend to throw light upon this most complicated problem, with its various interlocking processes. The mechanism of transformation of the various constituents of the leaves and other forest products will be discussed in the light of other studies by the senior author and his associates dealing with the transformation of natural organic materials both by pure cultures of microorganisms and by the complex soil population.

EXPERIMENTAL

A detailed discussion of the methods of analysis of natural organic materials is given elsewhere (Waksman and Tenney, '27). The application of these methods to the analysis of soil organic matter necessitated various modifications which will be published later. It is sufficient to point out here that it is essential to know the composition of the natural organic materials which are added to the soil before the various transformation processes brought about by microorganisms, and the nature of the soil organic matter which results, can be understood. From a practical standpoint it is quite sufficient to measure the course of ammonia and nitrate formation and CO_2 evolution, in order to have a good index of the rapidity of decomposition of the soil organic matter or of fresh organic materials added to the soil. One may also determine the reaction of the soil and its mineral composition. To understand the nature of the so-called forest "humus" and the reasons for its particular composition under different conditions and the mechanism of its decomposition, one should know first the various transformations to which fresh organic matter (whether leaves, twigs, roots and other tree products, or mosses, shrub products and other organic residues) is subject when brought in contact with the soil.

Composition of certain natural plant materials.

It is not at all essential to make a complete chemical analysis of all the plant constituents for the purpose of studying the processes of decomposition of these materials. At the present state of our knowledge of plant composition and of the methods of analysis of the various organic complexes present in natural plant materials, it is sufficient to be able to follow the course of transformation of those organic substances which occur most abundantly in the plant. For this purpose only proximate analyses will suffice. Such analyses have been developed by wood technologists, and such an analysis was proposed by the authors (Waksman and Tenney, '27) for the analysis of plant materials in the study of their decomposition in the soil. A modification of this analysis can be used quite readily for the determination of the nature and abundance of the constituents of soil organic matter, especially in those soils in which the organic fraction predominates over the inorganic fraction as in the case of peat soils or the upper layers of forest soils. No attempt is made to account for the presence of a large number of plant constituents (pigments, tannins, resins, etc.¹) which are present in the plant residues only in small concentrations. Attention will be largely directed to those plant constituents which make up the bulk of the organic matter which the soil receives either directly from the plant or through the agency of man. For this purpose, it is sufficient to divide the various plant substances into certain groups which have certain characteristics in common. Seven such groups have been used in the investigations reported here. These are:

1. The cold and hot water soluble plant constituents comprising the sugars, starches, organic acids, amino acids, certain water soluble proteins, etc.
2. Hemicelluloses, including the pentosans and the various hexosans insoluble in water, but soluble in dilute alkalis; they are also readily dissolved and hydrolized by hot dilute acids (1 to 4 per cent hydrochloric).
3. True celluloses which are dissolved in ammoniacal copper solution and in 65 to 72 per cent sulfuric or 39 to 42 per cent hydrochloric.
4. Lignins which are not acted upon by 72 per cent sulfuric or 42 per cent hydrochloric acids but are largely dissolved by alkalis under pressure.
5. The proteins. The "crude protein" fraction is obtained by subtracting the water-soluble nitrogen from the total nitrogen and multiplying the difference by 6.25.
6. Ether-soluble constituents, comprising oils, fats and waxes.²

¹ In some cases it is important to consider the alcohol soluble fraction (the extraction with ether is followed by extraction with 95 per cent alcohol). This fraction will include the pigments, tannins, resins, some of the waxes, etc. Some of the sugars and amino acids, which would otherwise be extracted in the cold water fraction as well as a certain part of the lignins, would then be included also in the alcohol fraction.

² See footnote 1.

7. Ash, comprising all the inorganic constituents of the plant material, not volatilized on ignition.

TABLE I. *Proximate composition of some natural organic materials*³

Plant material	On basis of dry weight						
	Pine needles	Oak leaves (green)	Oak leaves (mature yellow)	Hypnum moss	<i>Carex</i> (green part)	<i>Carex</i> (rhizomes)	Rye straw (mature, stems and leaves)
	Per cent	Per cent	Per cent	Per cent	Per cent	Per cent	Per cent
1. Cold and hot water soluble organic matter.....	13.02	22.02	15.32	8.41	12.56	3.18	9.90
2. Hemicelluloses.....	14.68	12.50	15.60	18.92	18.36	20.86	22.90
3. Celluloses.....	18.26	15.92	17.18	24.75	28.20	11.78	36.29
4. Lignin.....	27.63	20.67	29.66	21.13	21.08	41.74	19.80
5. Crude protein..	8.53	9.18	3.47	4.16	7.08	14.62	1.06
6. Ether-soluble portion.....	7.65	7.75	4.01	4.58	2.54	1.66	1.26
7. Ash.....	3.08	6.40	4.68	4.33	3.30	4.56	3.90
Total.....	92.85	91.44	89.92	86.28	93.12	98.40	95.11

Table I shows the analysis of several plant materials, four of which are forest products, namely pine needles, green oak leaves (picked from tree in autumn), mature oak leaves (recently fallen), hypnum moss (*Hylocomium paryetinum*); the analyses of the other three materials, namely the green part of *Carex*, the rhizomes of *Carex* and mature rye straw are given for comparison.

The results show that by this method of analysis we can account for 90 to 98 per cent of the constituents of practically all the natural plant materials, with the exception of the moss. This is probably due to the presence of various organic acids and certain substances related to the hemicelluloses which give non-reducing sugars on hydrolysis with dilute acids. The introduction of the alcohol-soluble fraction would also modify considerably the figure for the lignin in the moss.

It is interesting to compare the composition of the green oak leaves with the fallen mature oak leaves. The ash and nitrogen content and the amount of water-soluble (especially cold water) constituents, are considerably higher

³ These figures are not absolute. The plant materials will vary considerably in composition, depending not only upon the specificity of the plant, but upon the age of the plant, time of falling of leaves and needles, content of nutrients in the soil, type of soil, etc. It was found, for example, that two samples of needles of *Pinus strobus* collected in the same locality, two months apart, one from the broken twigs and one directly under the tree, comprising needles recently fallen, varied considerably in composition: the nitrogen content of one was 1.36 per cent, and of the other 0.38 per cent; the ether soluble fraction of the first was 7.65 per cent and of the second 11.50 per cent, etc.

in the green than in the mature leaves; the ether-soluble constituents are also somewhat higher in the former. The hemicelluloses, celluloses and lignins are higher in the mature than in the younger leaves. This confirms the results previously reported (Waksman and Tenney, '27) on the composition of rye plants at different stages of growth, where it has been shown that with the advance in the growth of the plants there is a gradual (percentage) decrease in the nitrogen, ash and fat content, as well as of the water-soluble portion, and a gradual increase in the pentosan, cellulose and lignin content. The composition of the plant influences the rapidity of its decomposition, the more mature plants decomposing more slowly than the younger plants.

A careful examination of the results of Kleberg ('27) on the composition of young and old leaves and needles of various deciduous and evergreen trees also reveals the fact that the green young leaves contain more nitrogen, less pentosan, less crude fiber and less methoxyl than old leaves. Combes ('27) explained the drop in the nitrogen content of leaves from 2.3 per cent when green to less than 0.9 per cent when mature by the transference of the nitrogen to the roots and stems.

The most striking difference in the composition of the leaves is found in the cold water soluble fraction. The green leaves contained 17.7 per cent of cold water soluble constituents of which 7.2 per cent was actual reducing sugar, while the mature leaves contained only 10.3 per cent cold water soluble constituents with 3.2 per cent reducing sugar. The nitrogen content of the cold water soluble fraction was also about twice as high in the green as in the mature leaves.

It may also be of interest to call attention to the difference in the composition of the green and growing part of the *Carex* plant and of the dead rhizomes. The differences observed in the case of the various constituents of the growing part on the one hand, and of the rhizomes on the other, is not merely a result of a difference in the composition of the young and old portions of the same plant but also a result of the attack of the rhizomes by various fungi, which were found to penetrate abundantly through the rhizomes and bring about considerable reduction in the cellulose content and an increase in the lignin and protein content.

The results presented in the analysis are of more than theoretical interest. A knowledge of the composition of the plant will enable us to foretell readily how the particular plant material will decompose when introduced into the soil. It will help to explain the various transformations brought about by microorganisms, the rapidity of mobilization of the nitrogen and the nature of the soil "humus," that will result from the decomposition.

It is sufficient to illustrate here briefly the decomposition processes in forest soil under aerobic and anaerobic conditions, with a free access of air and with a limited air supply. For this experiment the green oak leaves have been utilized.⁴ These were air dried, then added, in quantities equiva-

⁴The authors are indebted to Dr. H. Jenny for assistance in the collection of the material and in starting this experiment.

lent to 200 gm. of dry material, to earthenware pots containing 2,000 gm. quantities of white quartz sand. One group of pots received an optimum amount of moisture (60 per cent of the moisture holding capacity) and were kept aerobic; to another group of pots sufficient water was added to saturate the organic matter and the sand and make the conditions anaerobic. Some of the pots in both series received 10 gm. quantities of CaCO_3 and some received 5 gm. quantities of $(\text{NH}_4)_2\text{HPO}_4$. The addition of available nitrogen had no effect upon the decomposition of the leaves, which contained themselves enough nitrogen to satisfy all the needs of the microorganisms bringing about the decomposition. Had the fallen leaves been used in this investigation, the addition of available nitrogen would have had a decidedly favorable effect. The pots were covered with plates and placed in a thermostat kept at 25–28° C. Decomposition was allowed to proceed for 6 and 12 months, when aliquot samples were taken out for analysis. The data reported in Table II were calculated on the basis of the original 200 gm. portions of leaf material, or the total contents of organic matter in the original pots.

TABLE II. *Decomposition of fresh oak leaves under aerobic and anaerobic conditions*

	On the basis of original 200 gm. of dry leaf material								
	Original leaves	Aerobic preparations				Anaerobic preparations			
		After 6 months		After 12 months		After 6 months		After 12 months	
		No CaCO_3 No	CaCO_3 present	No CaCO_3 No	CaCO_3 present	No CaCO_3 No	CaCO_3 present	No CaCO_3 No	CaCO_3 present
gm.	gm.	gm.	gm.	gm.	gm.	gm.	gm.	gm.	
1. Water soluble organic matter....	44.04	10.52	6.46	6.53	4.72	11.06	9.07	6.78	5.35
2. Hemicelluloses....	25.00	6.62	5.85	5.55	4.74	22.95	22.72	12.81	7.45
3. Celluloses.....	31.84	6.01	4.57	4.76	3.01	28.70	25.27	15.35	14.95
4. Lignins.....	41.34	38.20	37.66	26.25	22.48	41.85	40.95	39.35	37.06
5. Crude proteins....	18.36	9.37	9.81	11.36	11.71	17.74	17.60	16.95	16.47
6. Ether-soluble portion.....	9.50	2.31	2.96	0.98	0.75	7.38	6.70	4.47	3.70
Total organic matter accounted for....	170.08	76.03	69.31	55.43	47.41	129.68	122.31	95.71	84.98
NH ₄ -N.....		0.143	0.046	0.033	0.018	0.012	0.004	0.004	0.008
NO ₃ -N.....		0.469	0.528	0.458	0.596	0	0	0	0
pH.....		4.93	6.13	4.82	8.03	6.50	8.19	7.22	7.42

The results show, first of all, that under aerobic conditions, both in the presence and absence of additional CaCO_3 , the leaves decompose very rapidly, more than half of the organic matter disappearing in 6 months. After 1 year of decomposition under optimum conditions less than one-third of the organic matter is left. The nitrogen is rapidly liberated as ammonia which is soon changed to nitrate. The water soluble constituents, the hemicelluloses,

celluloses and proteins, all decompose rapidly. The apparent slow reduction in protein content is due to the synthesizing activities of the microorganisms which build up new proteins. The lignins are the most resistant constituents of the plant materials. After six months decomposition there is only a very limited reduction in the lignin content; after 12 months, the decomposition is more definite. Two-thirds of the "humus" formed from the decomposition of leaves under aerobic conditions are found to consist of lignins and proteins. The microbiological flora of the aerobic mixture consisted predominantly of fungi; 400,000 fungi and 6,000,000 bacteria were found in 1 gram of sand-organic matter mixture not receiving lime; 600,000 fungi, 2,000,000 bacteria and 300,000 actinomyces in 1 gm. of the sand-organic matter mixture receiving CaCO_3 .

Under anaerobic conditions, the decomposition processes are considerably slower. Although the reaction of the medium never became too acid, only the water soluble constituents were at first attacked, while the other plant constituents were rather resistant to decomposition, especially the hemicelluloses and lignins. The crude proteins even increased at first somewhat in quantity due to the fact that a large part of the water-soluble nitrogen was changed into microbial protoplasm and became water insoluble. Even after 1 year of decomposition, the reduction in the protein content is very small; the difference between the protein in the original leaves and that in the decomposed material could easily be accounted for by the water soluble nitrogen. Only a trace of the nitrogen became liberated as ammonia even after decomposition for one year. It is of great interest to compare the rapidity of decomposition of the various plant constituents under aerobic and anaerobic conditions. The cold and hot water soluble substances disappear as rapidly under anaerobic as under aerobic conditions. The celluloses and hemicelluloses are decomposed very rapidly under aerobic conditions, where the fungi are largely active in the process, while under anaerobic conditions the rate of their decomposition is considerably slower; even after 12 months incubation at optimum temperature, half of the cellulose remains undecomposed; the hemicelluloses disappear somewhat more rapidly, especially in the presence of CaCO_3 . The ether-soluble substances are decomposed rapidly under aerobic and slowly under anaerobic conditions. The lignins are the complexes most resistant to attack by microorganisms; even under aerobic conditions, they decompose only very slowly, somewhat more rapidly when CaCO_3 is added. Under anaerobic conditions, they are very resistant and only a small part of the lignins has disappeared even after 12 months. The fact that only a trace of the nitrogen has become liberated as ammonia under anaerobic conditions is particularly striking. Practically all the nitrogen present originally in the leaves is found in the residual material. Here again, we find the lignins and the proteins as the two most important complexes of the residual organic matter, or the "humus." To this we must

add, of course, the celluloses, hemicelluloses and other constituents of the original plant material undergoing decomposition.

The results presented here point clearly to the mode of formation of forest humus and of the resistant forest peat, when the excess of water on the surface of the ground prevents rapid decomposition.

To compare the composition of this "humus" formed under controlled laboratory conditions with natural forest "humus," three forest soils were secured from Mount Desert Island, Maine.⁵ These soils were analyzed by the methods outlined above, in a manner similar to the analysis of natural plant products.

Soil A was obtained from a forest of northern hardwoods-spruce, in which hardwood leaves formed the great bulk of the material, I representing the surface layer (about 2 cm. in depth, Hesselman's F layer) and II the layer of organic matter below that (3 to 10 cm. in depth, Hesselman's H layer). B is taken from a forest of mixed coniferous and deciduous trees, III being the upper layer and IV the lower layer. C is obtained from a spruce forest with a heavy growth of hypnum moss (*Hylocomium paryetenum*). A microscopic examination of these soils revealed a great abundance of fungus mycelium forming one uniform mass with the plant residues. Actinomyces were found abundantly in soil A, but not in soils B and C. The analytical results of these soils are given in Table III.

TABLE III. *Proximate composition of natural forest "humus"*

	On basis of dry materials					
	AI	AII	BI	BII	CI	CII
Soil type.....						
Reaction, pH.....	5.6	4.9	5.1	4.4	4.4	4.3
Cold and hot water soluble fraction, %.....	5.80	2.73	5.03	4.66	5.14	3.63
Hemicelluloses, %.....	15.28	12.39	15.48	17.87	17.50	17.30
Celluloses, %.....	9.44	2.56	7.28	3.84	9.62	5.64
Lignins, %.....	39.30	50.39	38.38	37.29	42.26	44.88
Crude protein, %.....	8.29	7.51	8.02	7.04	6.84	5.15
Ether-soluble fraction, %.....	4.41	2.99	5.21	3.96	3.58	3.94
Ash, %.....	9.20	11.61	7.94	13.67	6.05	10.57
Total.....	91.72	90.18	87.34	88.33	90.99	91.11

The results obtained in the study of the composition of natural forest "humus" or the organic matter layers of forest soil fully confirm the theoretical considerations outlined above, as a result of the study of the decomposition of plant products under controlled conditions. Given a definite set of environmental conditions and a certain type of fresh organic matter, a

⁵ The authors are indebted to Mr. B. Moore and Dr. E. Melin for securing these samples of material.

⁶ The hemicellulose figure is considerably higher than the pentosan figure, as seen from the fact that AI contained only 6.39 per cent pentosan, AII—2.85 per cent, CI—4.69 per cent and CII—3.49 per cent.

definite kind of soil organic matter will result. The fact that the organic matter found in the forest soils contains a high percentage of cellulose and hemicellulose indicates that the decomposition processes have not proceeded far enough. By comparing the composition of the "humus" in the northern hardwoods-spruce forest (A) with the composition of the oak leaves (Table I), of the "humus" in soil B with the pine needles (Table I), and of the "humus" in soil C with the hypnum moss (Table I), one can readily recognize that the changes observed in the decomposition of oak leaves under aerobic conditions in the laboratory are quite the same as those that have taken place in nature in the formation of the forest "humus."

To compare the composition of the organic matter ("humus") found in a natural forest soil with that formed under controlled laboratory conditions from the decomposition of leaf material, some of the results presented in Tables II and III are summarized on an ash-free and moisture-free basis and presented in Table IV. These results point quite definitely to the similarity of the processes of formation of organic matter in nature and in the laboratory from the same or from similar plant products. The decomposition of the leaves in the laboratory (after 6 months) has advanced somewhat too far to be absolutely comparable with the results of the upper layer of the northern hards-spruce forest soil. This is demonstrated both by the higher lignin and protein content and the lower content of hemicelluloses, celluloses and of the ether-soluble fraction. The difference in the composition of the original material, the difference in the environmental conditions under which the decomposition processes have taken place, and possibly also a difference in the flora and fauna active in the decomposition in the forest soil and in the pot in the laboratory will no doubt account for the slight differences in the composition of the two materials.

TABLE IV. *Proximate composition of natural forest "humus" (hardwood forest) and of "humus" prepared in the laboratory by the decomposition of fresh oak leaves*

On basis of moisture-free and ash-free organic matter		
	Surface "humus" layer of hard- wood forest soil	Oak leaves decom- posed for 6 months, under aerobic conditions
Composition of "humus "	Per cent	Per cent
Water-soluble fraction	7.00	13.84
Hemicelluloses	18.52	8.71
Celluloses	11.44	8.00
Lignins	47.64	54.21
Proteins	10.06	12.33
Ether-soluble fraction	5.24	3.04
pH	5.60	4.93

The results presented in these studies point definitely to the conclusion that the term "humus" should not be applied to designate all types of organic matter found in forest soils, since it does not differentiate between (1) fresh, undecomposed organic matter, largely of plant origin; (2) organic

matter in the process of decomposition; (3) organic matter which results after a more or less complete decomposition of the natural organic matter and which consists of certain substances resistant to decomposition, of cells of numerous microorganisms and of decomposition products. The surface layer of the soil consists largely of fresh, undecomposed or slightly decomposed organic matter. The so-called "raw-humus" comprises various constituents of plant products resistant to decomposition (lignins, cutins, tannins, resins, waxes), in the process of decomposition (celluloses, hemicelluloses, proteins) and microbial cell substance, largely fungus mycelium (comprising synthesized proteins, hemicelluloses, etc.). The so-called "mull" types of soil are considerably advanced in the processes of decomposition, with a marked reduction of the celluloses and hemicelluloses, some reduction (total, not relative) in the lignins and a considerable increase in the microbial cell substance, which has undergone in itself considerable decomposition.

Organic matter in forest soils represents various gradations between the fresh organic matter and the fully decomposed organic matter which consists of certain plant constituents resistant to decomposition and various substances synthesized by the numerous soil microorganisms. It is absolutely incorrect, chemically as well as biologically, to apply the term "humus" to these various forms of organic matter. The use of this term merely tends to block further progress in our studies of the origin and nature of organic matter in forest soils.

SUMMARY

The organic matter of forest soils or forest "humus" should be considered in the light of the composition of the natural plant products which contributed to its formation and accumulation, the environmental conditions under which the decomposition of natural organic matter has taken place, and the nature of the microorganisms which have been active in the decomposition processes.

Forest "humus" is made up 1. of a number of the residual constituents, such as the celluloses, hemicelluloses, fats, waxes, etc., of the various plant products (leaves, twigs, roots, mosses, etc.) which are undergoing decomposition; 2. of the constituents of the plant products which are more or less resistant to decomposition, such as the lignins, cutins, tannins, resins, etc.; 3. of the microbial cells (fungus mycelium, spores, bacterial cells, protozoa, worms, etc.) synthesized in the process of decomposition of the natural organic materials continuously added to the soil; and 4. of the products of decomposition of the natural materials and cell products, such as organic and inorganic acids, ammonia, etc.

A series of methods have been developed which permit a comparison of the composition of the organic matter of forest soils with that of fresh undecomposed plant products and a careful accurate measurement of the nature of this organic matter or of the so-called "forest humus."

The use of alkalies and other reagents in determining the various "humic acids" and numerous other acids and so-called acids in the organic matter of forest soils is altogether unjustified. The very use of the term "humus" is questioned, since it does not represent, either chemically or biologically, any uniform substance or group of substances.

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RELATION OF SPAWNING OF THE OYSTER TO TEMPERATURE¹

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INITIAL SPAWNING OF THE SEASON

References to the relation between temperature and spawning of marine animals are numerous, but in no instance has there been prolonged investigation of the breeding periods of one species with continuous recording of the temperature. The voluminous collection of data in the notes of Lo Bianco ('09), and in the "Plymouth Marine Invertebrate Fauna" ('04), while in a general way fixing spawning periods as associated with particular temperatures, do not yield exact information as to the minimum temperature at which spawning of a given species will occur, nor do they show how long a latent period must elapse after the critical temperature is reached before spawning actually is begun (Nelson '28).

Orton ('20), states that spawning occurs in the European oyster, *Ostrea edulis*, when the temperature reaches 15–16° C.; and he points out that whereas the oyster breeds in Norway for only a short time in August, if at all, this same species in the Gulf of Toranto is actively breeding from April to October. The American oyster of the Atlantic Coast, *O. virginica* Gmelin, may spawn in the Gulf of Mexico from March or April till late summer (Moore, '07); whereas in Nova Scotia spawning occurs during two or three weeks in late July or early August in favorable years, or not at all in cool years when the temperature fails to attain 20° C. (Nelson, J., '17). The Australian oyster *O. cucullata* has been shown by Roughley ('26) to spawn only during warm years over the northern portion of its range. Apparently there has been no adaptive adjustment to lower temperature at the northern end of the ranges of the species of this genus, or to the higher ones at the southern extremities of distribution.

The American oyster of the Atlantic Coast falls in the 20° C. group of lamellibranch molluscs with respect to its spawning temperatures (Nelson, '28). How long after this temperature is reached, and how much heat must be received, before spawning actually is begun? The investigations here recorded cover a period of ten years, with an attempt at a mathematical analysis of the data for the last four years. They include temperatures taken by standard immersion thermometers and by a calibrated, frequently checked,

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thermograph situated in Barnegat Bay; daily plankton examinations of the water; and weekly examinations of the gonads of the oysters, detailed account of which will be found elsewhere (Nelson, '20, '27).

Mass spawning occurs in the oyster, involving often thousands of individuals. As I have shown with the aid of kymograph tracings (Nelson, Rpts. for '21, '22), the shells in the male gape with relaxation of the adductor muscle while a stream of spermatozoa issues with the excurrent water. In the female, rhythmic contractions of the adductor muscle force water from between the shells carrying out great numbers of eggs. I have also shown (*l. c.*) that raising oysters to a position just under the surface of the water where they come directly under the influence of the sun's rays will induce spawning. These field observations have been confirmed by Prytherch ('24) and by Galtsoff ('26) in the laboratory.

Long experience at this laboratory has shown that spawning of the oyster in nature occurs always on rising temperatures and during or shortly after the flood tide.² The time of spawning as indicated in this paper has been determined, after finding the one day old oyster larvae in the water, by tracing back through the preceding 24 hours to the time when sharply rising temperatures have coincided with the late flood tide.³

Figure 1 shows, for the years 1924 to 1927, the average mean weekly temperatures of the water on the bottom of Barnegat Bay over the period preceding and following active spawning of the oyster. These temperatures were determined by planimeter from the area enclosed under the temperature curve on the thermograph records (*cf.* Hartzell, '19). Figure 2 is a direct reproduction of the thermograph records from the time the temperature reached 20° C. until spawning was begun. Temperatures taken every 2 hours from the thermograph record have been plotted in figure 3 with an enlarged vertical scale, and a triangle of equal area has been constructed on the same base line of elapsed time. The data shown in figures 2 and 3 satisfy the theoretical requirements of the problem in that with the shortest elapsed

² Objection may be raised that it is difficult to be sure of the source of oyster larvae found in the water. Since Barnegat Bay is a small, almost landlocked, estuary with a tidal fluctuation between 4 and 6 inches with no oyster beds of importance within 20 miles, there is no possibility of the introduction of oyster larvae from outside sources.

³ Orton ('25, '26) reports a lunar periodicity in the breeding of *Ostrea edulis*. It has not yet been shown that the shedding of eggs into the gills of an incubatory lamelibranch such as *O. edulis* is controlled by the same factors as those which govern the release of ova and spermatozoa in a non-incubatory form such as *O. virginica*. Even if the two processes be induced by the same stimuli, Orton's paper ('26, Fig. 3) shows the probability of the effect of temperature quite independent of the lunar cycle. The water temperatures given in his figure 3 show that spawning occurred at or just before the peak of rising temperature in a manner quite identical with our own experience. The investigations of Fox ('23) show that caution must be used in connecting periods of reproductive activity with lunar cycles, until the effects of temperature and of other factors have been ascertained.

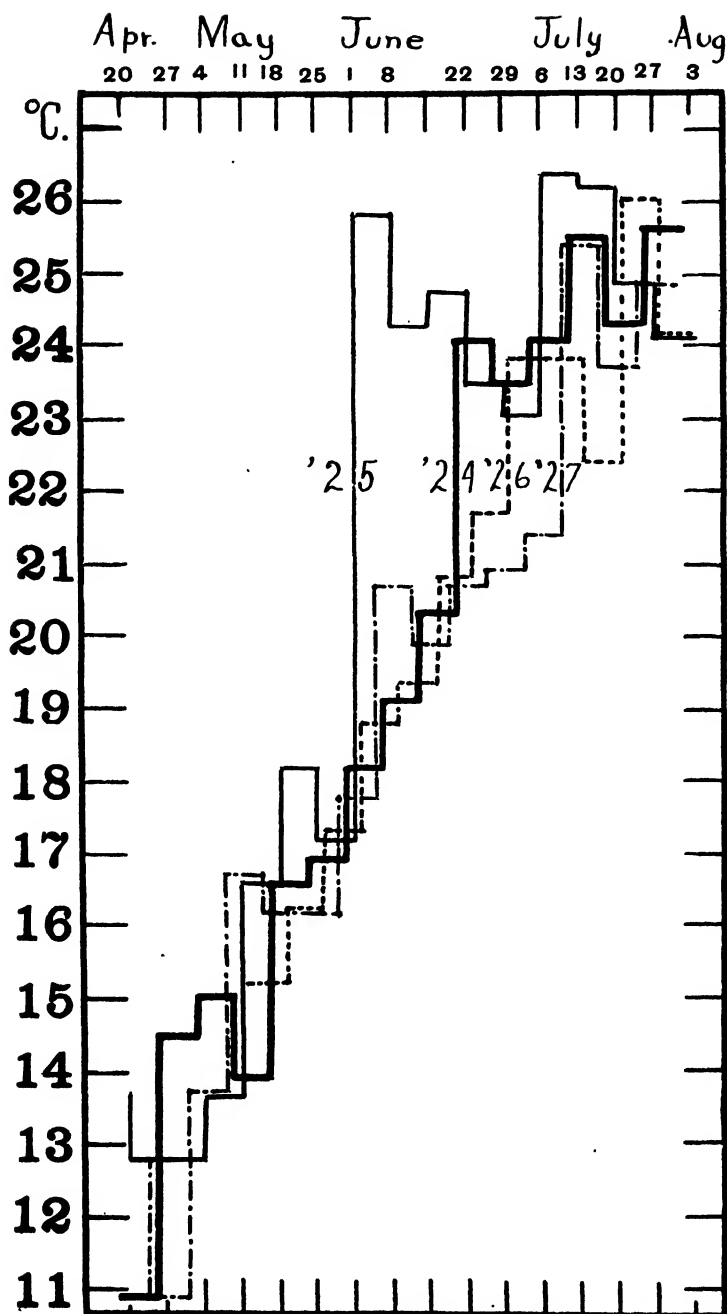


FIG. 1. Water temperatures at the bottom of Barnegat Bay, New Jersey. Heavy line, 1924; lighter line, 1925; dotted line 1926, dash-dot-dash line 1927. Mean temperature for each week computed with the aid of a planimeter from the area enclosed below the temperature line on the thermograph record.

time, 52 hours, the largest amount of heat above 20° was delivered, and the highest temperature at the time of spawning was attained. With the longest elapsed time, 94 hours, the smallest amount of heat above 20° was received and the spawning occurred at the lowest temperature observed during the four years.

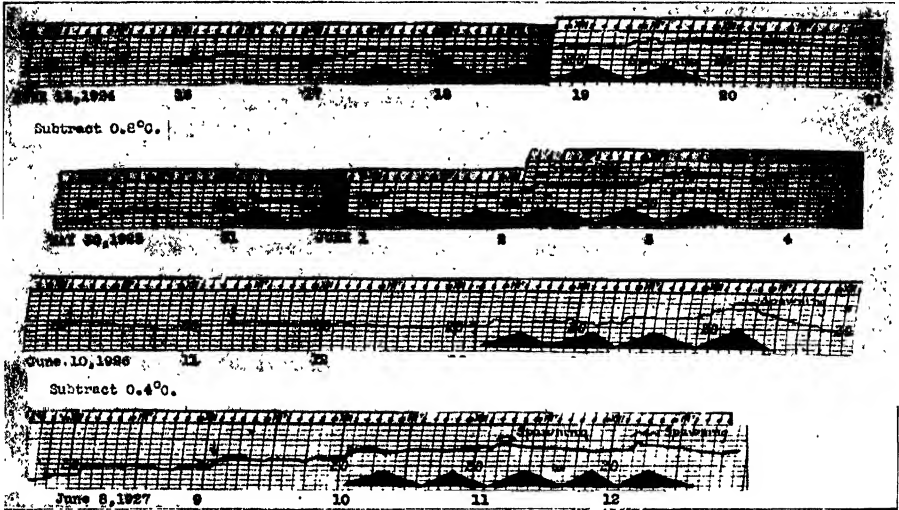


FIG. 2. Reproduction of thermograph records for four years of the water temperatures at the bottom of Barnegat Bay from the attainment of 20° C. until the onset of oyster spawning. Tidal movements as determined from a self-registering gauge are shown by the black triangles; high tides at the crests, low tides at the troughs. A correction of -0.8° C. must be applied to the 1924 line and of -0.4° C. to the 1926 line to give the correct temperatures.

The figures for 1925 require further explanation. During the first week of June of that year occurred a wave of unusual heat which averaged some 8.3° C. above normal and broke all records of the Weather Bureau for the State for this time of year. As a result of this great heat the bottom waters of Barnegat Bay were warmed from 18° to 27° C. in 5 days, and the oysters spawned apparently in two groups: those in shallow water after 48 hours and those in deeper waters after 74 hours. Strong convection currents were set up by the rapidly warming water, and it is doubtful whether the behavior of the oysters at this time can be considered typical. The two groups of spawning oysters have been considered separately in figures 3 and 4.

Since the oyster will spawn at 20° C., how long a period must elapse before spawning occurs if the temperature never rises above this figure? In other words, if the area of the triangle of "excess heat above 20° " approaches zero? By plotting the reciprocal of the absolute temperature as determined from the height of the perpendicular side of the triangle, against the logarithm

of the reciprocal of the elapsed time, three points are obtained which lie on a straight line, figure 4. The points for the two groups of oysters in 1925 lie almost equidistant on either side of this line. The ordinate raised at 20° intersects this line at an elapsed time of approximately 100 hours. Hence it is to be expected that in northern waters where the temperature during many years barely attains 20° C., the elapsed time would approximate 4 days.

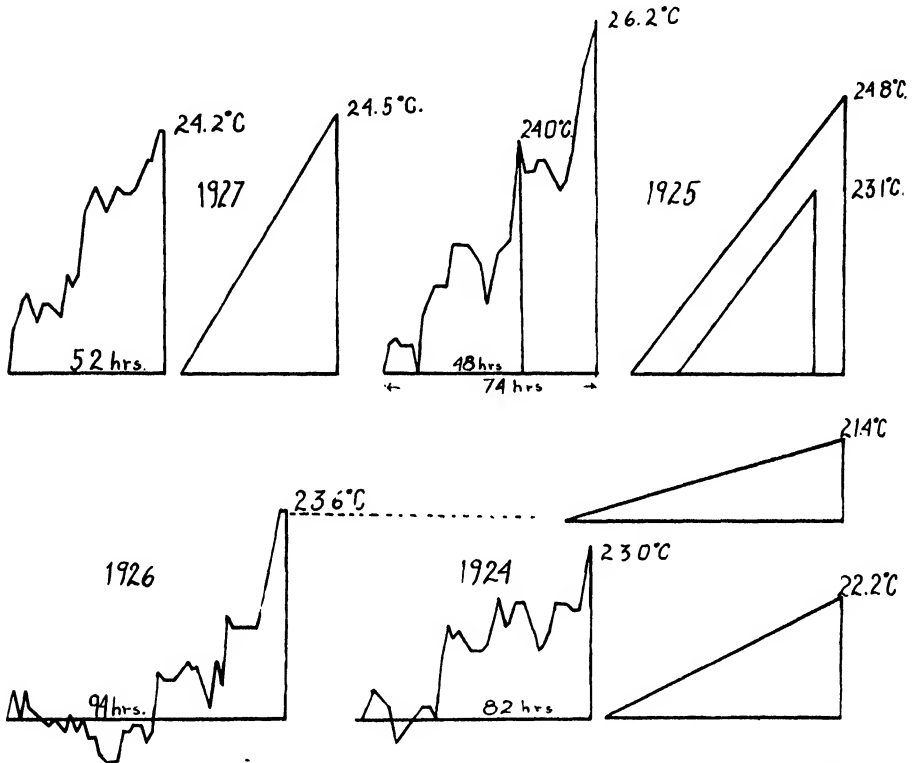


FIG. 3. Data from figure 2 replotted on enlarged vertical scale, temperatures being taken at 2-hour intervals. The triangles represent the areas of the adjoining figures as determined by a planimeter, drawn to the same base lines of elapsed time. The figure at the top of each temperature curve is the actual temperature in degrees C. attained during the spawning period. The figure at the apex of each triangle represents in degrees C. the "reduced" temperature, or measure of the slope of the temperature curve as determined from the height of the perpendicular.

It is supposed, in this interpretation, that once the critical temperature, 20° C., is reached a "trigger" mechanism is released which requires some hours for its consummation; and that the speed of the underlying processes is governed by temperature. Examination of figure 2 shows that coincidence of flood tide and sharply rising temperatures above 20° C. occurred in 1924 from 6 to 10 P.M. June 17; in 1925 during the afternoon of June 1; and in

1926 during the evening of June 14, and yet no spawning took place at these times. Prytherch ('24) records spawning at temperatures from 20 to 24° C. of oysters brought to shallow tanks from the depths of Long Island Sound where spawning temperatures are reached in only one year out of ten. Un-

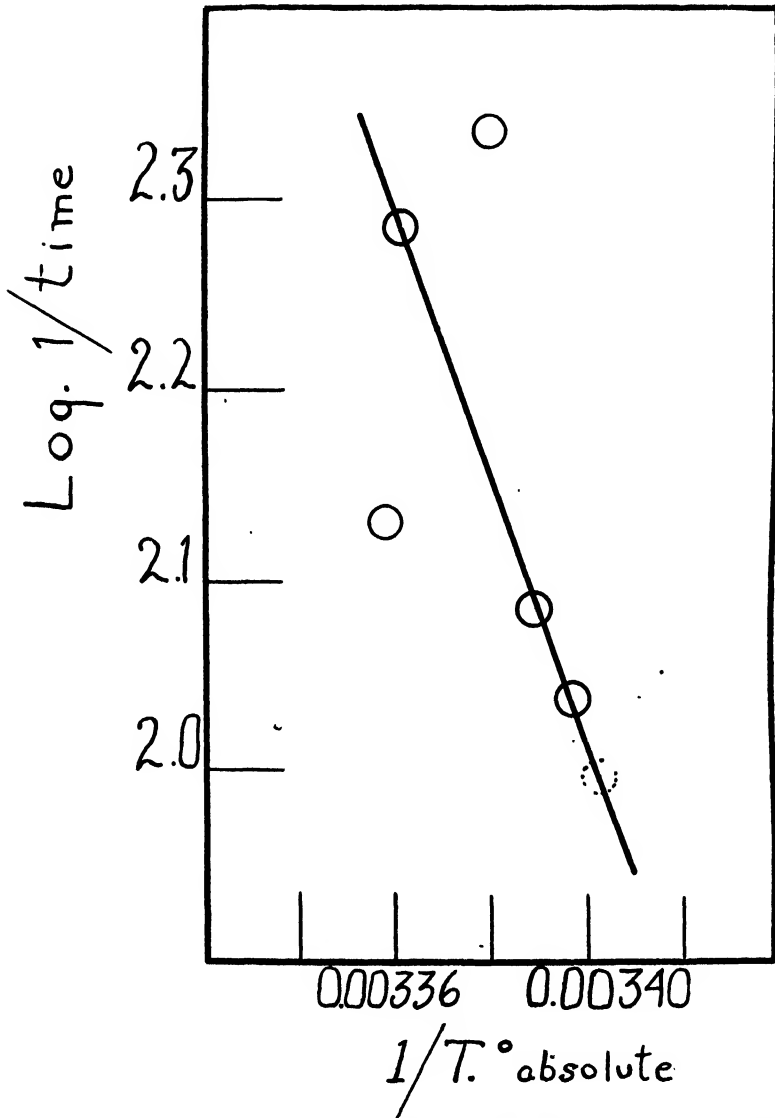


FIG. 4. The relation of temperature to time required before initiation of spawning of the oyster. The temperature is determined from the height of the perpendicular sides of the triangles in figure 3, while the time represents the number of hours after the water reaches 20° C. until spawning is begun. The dotted circle represents the intersection of the ordinate erected at 20° with the straight line.

fortunately there is no definite record of the temperatures to which these oysters were subjected before their removal, nor is the time between removal and spawning indicated.

TABLE I. *The number and condition of sexual maturity of oysters in Barnegat Bay, 1924*

	Mean water temperature ° C. preceding week	Male	Female
April 18....	9.1	4—sperm mother cells no spermatozoa. 1—active spermatozoa tubules distended.	Early oocytes, no yolk.
April 26....	10.9	2—sperm mother cells 2—active spermatozoa, tubules distended.	8—Early oocytes no yolk.
May 2.....	14.1	3—very early; few sperm mother cells. 1—distended with active spermatozoa, tubules very prominent.	10—early oocytes no yolk. 1—trace of yolk in oocytes.
May 10.....	15.0	2—sperm mother cells fragmenting; no active spermatozoa.	4—clear oocytes no yolk. 6—early ova, majority with yolk. Tubules distinguishable in 1.
May 17.....	13.9	4—sperm mother cells fragmenting; no active spermatozoa.	4—clear oocytes, no yolk. 4—early ova, majority with yolk. Ova half filled with yolk in 1.
May 24.....	16.6	1—sperm mother cells fragmenting. 1—50% in metamorphosis to active spermatozoa.	2—clear oocytes, no yolk. 6—ova show $\frac{1}{2}$ – $\frac{3}{8}$ yolk deposited. Tubules swollen in 1.
May 31.....	16.9	2—sperm mother cells fragmenting. 1—many active spermatozoa.	2—early oocytes, no yolk. 6—early ova $\frac{1}{2}$ – $\frac{3}{8}$ yolk deposited, 1 approaching ripeness.
June 6.....	18.2	2—very early spermatozoa, non-motile. 2—active spermatozoa, gonad $\frac{3}{4}$ filled.	1—early oocytes, no yolk. 7—early ova from a trace to $\frac{3}{8}$ yolk filled. Many clear oocytes among them.
June 12.....	19.2	2—active spermatozoa, tubules distended.	1—clear oocytes similar in size and appearance to those of April 26. 9—early to ripe ova, eggs from $\frac{1}{2}$ filled to full of yolk. Tubules swollen and cover most of gonad in 6.
June 16.....	18.5	5—active spermatozoa. Gonad distended and yielding milt on pressure in 3.	1—clear oocytes, no yolk. 6—early to ripe eggs, gonad distended in 1.
June 19.....	20.3	No males procured.	1—clear oocytes, no yolk. 4—early ova, half filled with yolk. 6—ripe, majority of eggs appear ready for spawning. 1—spawned.

The examination of the gonads of oysters from week to week, beginning in March, shows that active spermatozoa may be found in a few oysters at temperatures as low as 9° – 10° C., Table I. The deposition of yolk begins at temperatures approximating 15° C., with subsequent maturing of the ova at temperatures between 18° and 20° C. An outstanding fact in these observations has been the wide difference in the degree of maturity of oysters taken side by side from the same bed, necessitating caution in interpreting the behavior of these animals in the laboratory.

The effects of temperatures just under 20° C. are at present unknown. The data from the 1926 temperature curve in which "subcritical" temperatures occur twice for appreciable periods, indicate that development of the sexual products preparatory to spawning continues even at these lower temperatures, making possible a quick response when once the temperature rises above 20° C. It is to be expected that oysters which have been living at temperatures slightly below 20° C. for approximately one week will spawn quickly on being subjected to sharply increasing temperatures.

SUBSEQUENT SPAWNING DURING THE SEASON

After each wave of spawning, in nature, subsequent spawning usually occurs only after some days and then always on rising temperatures.⁴ The observed increase in temperature necessary to induce spawning at temperatures above 20° C. is close to 2° C., and to have the necessary stimulating effect the increase must occur within relatively a few hours. Later spawnings, therefore, occur usually at temperatures above that which caused the initial spawning of the season (Table II).

TABLE II. *Dates and temperatures at oyster spawning in Barnegat Bay*

	Dates of spawning	Mean average temperature 24 hours preceding spawning	Maximum temperature reached during spawning period
1924	June 19	22.5° C.	24° C.
	June 24	23.2	25.3
	July 7	22.8	26
	July 8	25.3	27.4
1925	June 3	23.4	26.1
	June 6	27.6	29
	June 27	23.6	24.2
	July 7	26.5	27.2
1926	June 15	21.6	23.7
	June 25	21.9	23.3
	July 10	24.5	26.9
	July 11	26.4	28.3
1927	June 11	23.4	24.6
	June 12	23.6	24.8
	July 8	21.2	23.6
	July 12	22.4	24.3
	July 13	23.9	26.8
	July 27	24.5	26.2

⁴ Galtsoff ('26) finds that oysters may be induced to spawn in the laboratory by a sudden increase in temperature of the water.

The spawning of July 7, 1924, was preceded by a gradual rise in temperature from a minimum of 21° C. on July 2. As seen from Table II, the maximum temperature during the last spawning of the season, on July 8, was 3.4° C. higher than that found during the initial spawning of the season. The spawning of July 10, 1926, was preceded by a period of cool weather with a minimum temperature of 20.7° C. on July 6. The last spawning of this season took place July 11 with a maximum temperature of 28.3° C., or 4.6° C. higher than that of the first spawning of the summer. As would be expected, therefore, in seasons of premature warmth followed by cool cloudy weather for the remainder of the summer, later spawnings may not follow the initial one, even though the temperature remains above 20° C. Following a cold summer unshed spawn may be found in the oysters even into the winter months.

The temperature figures for July 7 and 8, 1924, for July 10 and 11, 1926, and for July 12 and 13, 1927 illustrate clearly how still higher temperatures superimposed upon an already high spawning temperature will induce further spawning. In 1924 and 1926 this July spawning constituted the last general spawning of the season, all oysters participating therein becoming practically spawned out. Of those oysters which failed to spawn on the first day many were forced into spawning by the still higher temperatures of the day following. Due to the unusually low temperatures during 1927 as shown in Figure 1 some oysters were so backward in their development that the last general spawning was delayed until July 27th.

HOW DOES RISE IN TEMPERATURE INDUCE SPAWNING?

The mechanism through which a rise in temperature induces spawning in the oyster is not known. Bearing upon this are the observations of Galtsoff ('26) that both male and female oysters can be made to spawn by increasing the temperature of the water; whereas spawning in the female may be induced at constant temperature by the addition of sperm. Crozier ('22) demonstrated a similar relationship of the sexes in *Chiton*. Galtsoff, *l. c.*, has shown that after spawning a female oyster is for two days immune to the presence of sperm. Where spawning in nature occurs on successive days the second spawning is probably by oysters which, though not induced to begin spawning by the temperature of the first day, were stimulated to spawn by the still higher temperatures of the following day. From my own observations in New Jersey waters, only a relatively small proportion of the oysters present take part in the first spawning of the season. Not only does a much larger proportion of the oyster population engage in the later spawnings but each oyster involved throws out a larger proportion of its sexual products than is the case during the first or preliminary spawning of the season.

SUMMARY

The American oyster *Ostrea virginica* Gmelin spawns after the water temperature reaches 20° C., over all parts of its range, with no adjustment to the extremes of its distribution.

The length of the latent period after 20° C. is attained, before spawning occurs, bears a definite relation to the slope of the temperature curve.

Subsequent spawnings occur only after still higher temperatures have been attained, the increase necessary being approximately 2° C.

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REVEGETATION OF ILLINOIS COAL STRIPPED LANDS

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PRODUCTION OF BARE AREAS BY COAL STRIPPING OPERATIONS

Areas in Illinois were bared by coal stripping operations as early as 1866, but development of the industry, an interesting account of which appeared in the Coal Catalog ('26), was delayed until the invention of the large revolving stripping shovel in 1911. The present rapid expansion of the industry and consequent increase in waste lands present an important and interesting problem in conservation. The ecological study here reported represents an attempt to attack the problem from the standpoint of the natural revegetation of these waste lands.

Culver ('25) estimated the total area in Illinois available for stripping at 287 square miles. His map of the distribution of these areas is reproduced as figure 1. They occur along the margin of the coal field, with the exception of certain valleys where erosion has removed a part of the overburden. Commercial stripping operations are now in progress in Vermilion, Williamson, Perry, Fulton, Saline, Jackson, Richland, and St. Clair Counties. A check by the writer in 1926 indicated an accumulation of probably 3,000 acres of land laid waste in the process. Prior to stripping, these lands were generally in cultivation; although portions of the valley strippings, especially in Vermilion County, were forested. These forests in Vermilion County have been described by McDougall ('18b).

The material which overlies the coal and which goes to make up the ridges is highly variable both in thickness and in character. It presents a complex of preglacial, glacial, and postglacial action, and no one profile may be given as representative of the overburden within a single mine, much less throughout the stripping fields of the state. Essentially the same types of strata are present above all of the coal beds¹ of the state now being stripped, although there is considerable variation in the proportion and arrangement. Figure 2 presents something of the nature and variations of the strata commonly present.

The stripping shovel deposits the overburden material in the form of long parallel ridges commonly known as "spill" banks. Irregular action of the stripping shovel results in unequal mixing of the strata and leaves

¹ The No. 6 coal bed is the one most commonly mined in the state, although the No. 5 bed in Fulton and Saline Counties and the No. 7 bed in the Danville region of Vermilion County are of considerable importance.

patches of shale, till, clay, and waste coal exposed on the ridges. The slopes of the newly formed ridges are generally steep, and erosion is rapid where much till is exposed at the surface. Long wire stakes placed in the summits of newly formed ridges of this type indicated a lowering of about two feet

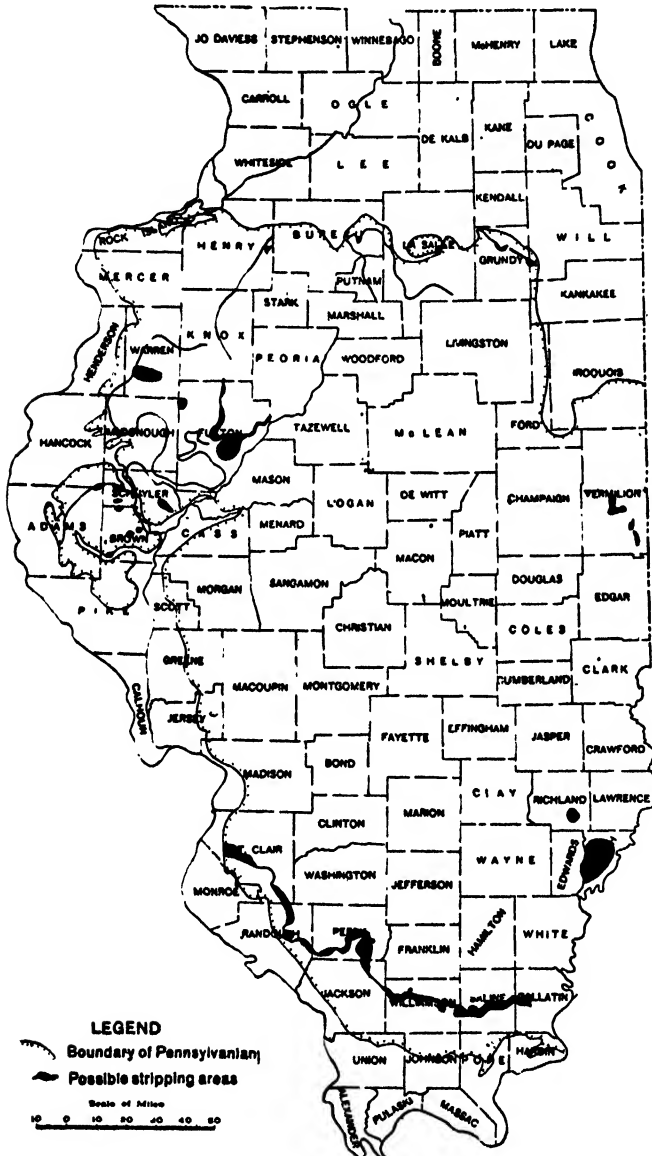


FIG. 1. Map of Illinois, showing location of possible stripping areas. The solid lines within the boundary of the Pennsylvanian system represent the line of outcrop of the several coal beds. Courtesy of the Illinois State Geological Survey.

during the first year. The surface of ridges containing large amounts of shale is very hard and erodes very slowly.

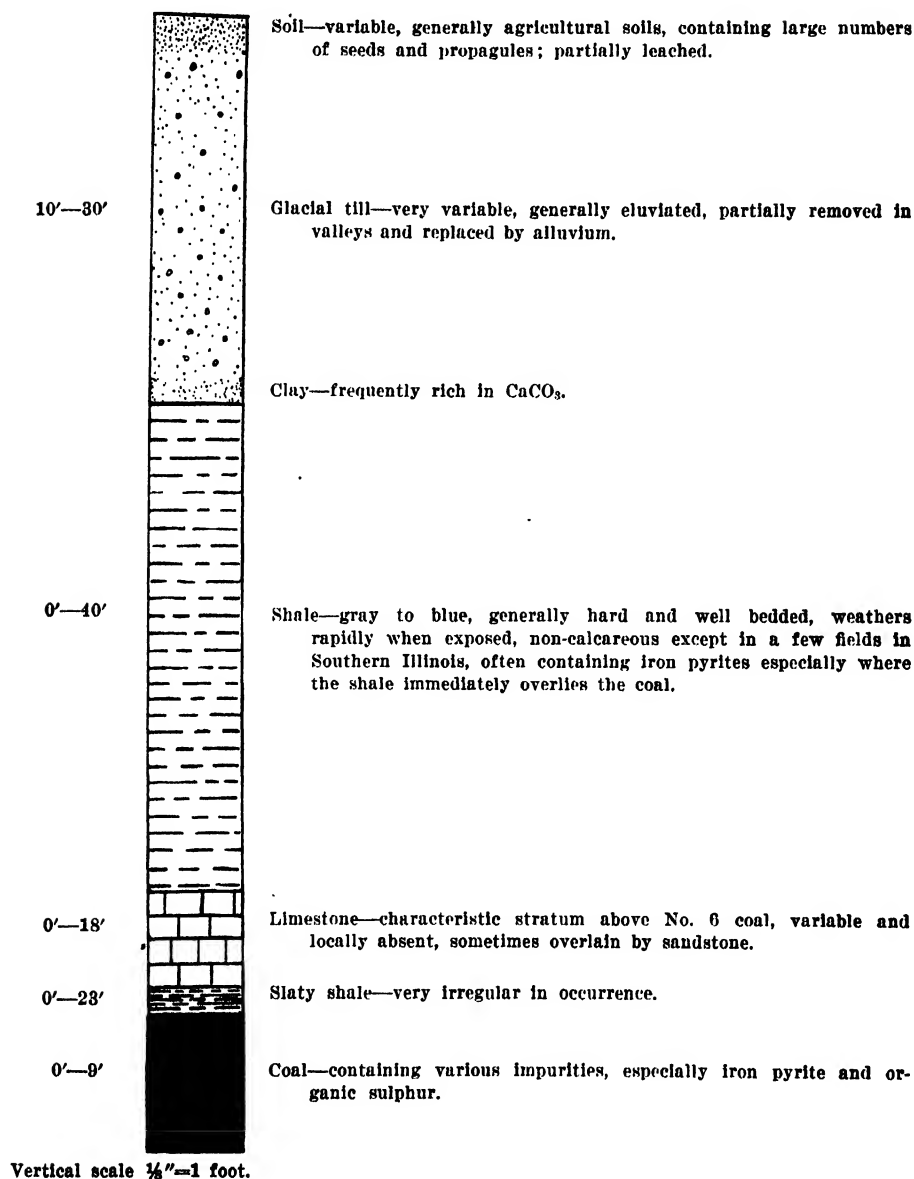


FIG. 2. Profile of the overburden showing the horizons commonly present in Illinois strip mines. (The diagram is based on the average thickness of the horizons in the various stripping fields. The figures at the left of the diagram represent, in feet, the extremes encountered.)

GENERAL VIEW OF STRIPLAND VEGETATION

The vegetation of coal stripped lands presents a confusing aspect, and gives proof of the marked diversity in edaphic factors. The vegetation cover is not continuous, being interrupted by numerous bare areas irregular in size, distribution, and outline. All gradations between entire failure and luxuriant growth are in evidence. While the aspect over considerable areas is dominated by *Polygonum pennsylvanicum*, *Melilotus alba*, or *Lactuca canadensis* and *L. scariola*; many herbaceous species form communities on the spill banks. Scattered colonies of the smaller woody plants, *Rubus occidentalis*, *Rubus villosus*, *Rubus* sp. (blackberries), *Tacoma radicans*, *Rhus glabra*, *Sambucus canadensis*, *Vitis rupestris*, *Amorpha fruticosa*, and *Cornus amomum* are common, the last three being limited to the low moist areas.²

To the above aspect must be added the trees—*Populus deltoides*, *Platanus occidentalis*, *Acer saccharinum*, *Fraxinus pennsylvanica*, *Ulmus americana*, *Salix nigra*, and *Diospyros virginiana* (southern Illinois), scattered stands of which are developing in numerous places along with the herbaceous vegetation. Open stands of cottonwoods and sycamores are present in portions of all of the older stripping fields of the state. Young cottonwoods also mark the high water levels, and, together with willows, form heavy stands in the vicinity of some of the ponds.

The hydrophytic vegetation also reflects differences in habitat conditions. While *Typha* swamps are numerous in the depressions between the ridges, in many of these the plants never attain normal size and appearance; still others remain barren. The same is true of the shallow ponds, some of which are nearly filled with *Myriophyllum* and *Potamogetons*, while others show little growth, and a few are practically devoid of life. *Potamogetons* grow in the marginal waters of most of the deep ponds to a depth of about five feet.

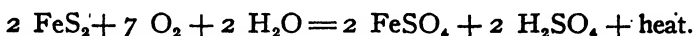
FACTORS CONTRIBUTING TO THE ACIDITY OF STRIPLAND SOIL MATERIAL

Early in the study it was noted that plants do not grow about the disintegrating iron pyrite lenses which are a common feature of coal stripped lands. The exposed surface of the pyrite and the soil material immediately about it always gave a strongly acid reaction. The acid was found to be sulphuric. The spontaneous combustion of these pyrites on many of the ridges afforded evidence of their oxidation when exposed to the air.

Parr and Kressman ('10) have shown that sulphur is always present in coal in amounts varying from .1 per cent to 8 per cent. According to these authors, "Coals of Illinois have, in the larger number of cases, iron pyrites averaging over 6 per cent." Powell and Parr ('19) state that sulphur occurs in coal in four forms, two of which are inorganic, and that FeS_2 (pyrite and marcasite) is the readily oxidizable form. Yancey and Fraser ('21)

² In the plant names Gray's Manual (seventh edition) has been followed instead of citing the authority for each name.

found that extreme irregularity of distribution is characteristic of the pyritic sulphur of coal in the bed, the coarse pyrite being much less uniformly distributed than the finely disseminated forms. It has been shown that the pyrite and marcasite sulphur is oxidized to ferrous sulphate and sulphuric acid as indicated by the equation:



Li ('26) has found that while marcastic tends to break down more readily than pyrite, forming a higher percentage of small particles, the rate of oxidation of both is inversely proportional to the diameter of the particles and directly proportional to the temperature. High textural moisture and a free stream of oxygen saturated with moisture were found to increase the rate of oxidation. The rate of oxidation of sulphur has also been studied by Stephenson ('26) and by Simon and Schollenberger ('25). According to these authors and to Powell and Parr ('19) and Li ('26), there is some evidence that sulphur bacteria are important agents in bringing about this oxidation.

At United Electric Mine No. 1 in Vermilion County one car load of coarse pyrite is picked from about twenty cars of coal. During the war the pyrite was cleaned and used for the manufacture of sulphuric acid. It is now loaded into empty cars and carried back to the strip pit, where it is dumped along the ridges with the idea of burying it to prevent firing. Although variable in distribution, the total amount of pyrites returned in this manner is very great where this method of disposing of the pyrite is practiced. There is abundant evidence that much of this remains on the surface of the ridges or at shallow depths for a long period, gradually oxidizing with the formation of ferrous sulphate and sulphuric acid. A strong odor of SO_2 is sometimes present and the pyrites occasionally fire. Some preliminary experiments in which soil thermometers were placed in the ridges of high and low apparent pyrite content showed constantly slightly (about 4°C.) higher temperatures in the former. It is evident, however, that the return of pyrites to the ridges in this manner does not alone account for the acidity of stripland soils, since some companies practice picking in the strip pit and others sell the coal mine run. Large areas in these fields were likewise found to be strongly acid. In some of these ridges coarse pyrites were common, while in others few were evident.

Attention was given the shales as a possible source of the acid. As indicated in figure 2, these shales form a large part of the overburden, accounts of which are contained in the publications of Cady ('16), ('17), ('19), ('21), Kay ('15), and Kay and White ('15) on the geology of the Illinois coal measures. It was noted in the valley strippings that the ridges along the bluffs, consisting largely of heavy shaly overburden, are highly acid and have failed to revegetate. When tested with LaMotte colorimetric indicators and HCl ,

the shales varied greatly in reaction. Many were strongly acid, some were neutral, and others gave an alkaline reaction and effervesced freely. The shale immediately above the coal gave the most acid reaction, the acidity decreasing with increase in height above the coal bed. Coarser pyrites were in evidence in the roof shales, and close examination revealed considerable amounts of fine disseminated pyrite. Stull and Hursh ('17), who studied the roof shales and floor clays available in Illinois coal mines with reference to their suitability in the clay industry, reported the presence of pyrites in the first few feet of shale in a high per cent of the samples examined. The weathering of the shales on the spill banks exposes the fine pyrite, which is rapidly oxidized. It seems likely that the pyrite in shale constitutes a rather important factor in the production of the acid in the spill banks.

ACIDITY OF THE SURFACE SOIL IN RELATION TO THE DISTRIBUTION OF VEGETATION

Numerous field tests of the surface soils made at irregular intervals on the ridges with colorimetric indicators gave a range of pH values from less than 3.5 to 9.0. As pH 3.5 is below the limit where most vegetation succeeds, a lower indicator such as thymol blue was not used. A composite of some of the more acid samples was found to be pH 2.6 by the hydrogen electrode method. Such a wide range of hydrogen ion concentration may be encountered within a very small area, as shown in figure 3, which represents the combined vegetation, topography, and hydrogen ion concentration maps of a plot 100 feet square located along the margin of one of the largest bare areas in the old Butler Ballast Company strippings in Vermilion County.

The plot was staked out with wire stakes, subdivided into one hundred small plots ten feet square, and later fenced with rabbit proof fence. The diagonals were marked out in each plot, and the pH of the surface soil measured half way out on each semi-diagonal. This gave an equal distribution of the four hundred tests and made it possible to reestablish the points whenever it is desired to repeat the tests. The upper six inches of surface soil material at each point was mixed by stirring with a narrow trowel, and a sufficient amount placed in a six inch test tube to fill it to a depth of about one and one half inches. The tube was then nearly filled with distilled water, shaken and placed in a nearly vertical position for the soil to settle. The clear solution was poured into vials and tested by adding a drop of the LaMotte color indicators. Comparison by other methods showed that any error due to not keeping the material in suspension was very small. Some additional errors were doubtless introduced in judging colors in the open light, but the method was probably sufficiently accurate for the purpose.

A definite correlation is shown between the vegetation and the hydrogen ion concentration. Vegetation is lacking or scant on the most acid portions, generally becoming well established at about pH 5.0, and forms a heavy

stand on the nearly neutral soil. The failure of vegetation is so definitely correlated with acidity in this small experimental plot that it seemed worth while to test this hypothesis over the striplands more generally. Accordingly, pH measures were obtained at fifty locations widely distributed over the United Electric mines in Vermilion County. At each location two tests were made, one where the vegetation is thriving, the other in an adjacent nearly or entirely barren spot. The results of these tests are shown in Table I.

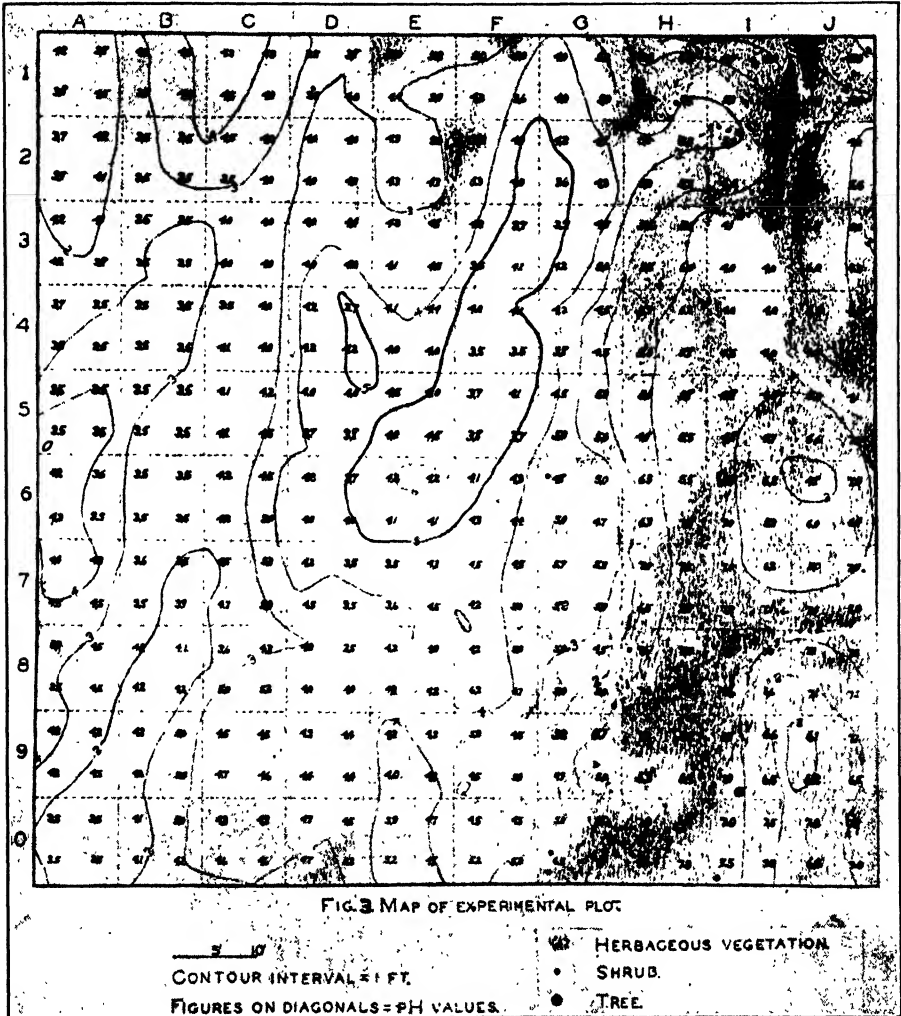


Fig. 3. Vegetation, topography and hydrogen ion concentration of a plot 100 feet square along the margin of one of the largest bare areas in the old Butler Ballast Co. strippings in Vermilion County.

TABLE I. Comparison of the hydrogen ion concentration of the surface soil in vegetated and adjacent bare areas

Vegetated Area		Adjacent Barren Area	
Vegetation	pH	pH	Vegetation
<i>Ulmus americana</i> , <i>Poa pratensis</i>	8.0	4.1	None.
<i>Tacoma radicans</i> , <i>Solidago</i> , <i>Polygonum</i> , <i>Cassia</i>	5.3	4.2	None.
<i>Poa pratensis</i>	8.0	5.0	Thin stands of <i>Cassia</i> , <i>Setaria</i> , <i>Poly-</i> <i>gonum</i> .
<i>Poa pratensis</i>	7.6	4.3	At edge of <i>Cassia</i> margining the grass
<i>Poa pratensis</i> , <i>Melilotus alba</i>	7.7	5.0	Scattered <i>Cassia</i> plants.
<i>Melilotus alba</i>	7.1	4.5	Scattered <i>Cassia</i> plants.
<i>Polygonum</i> , <i>Echinochloa crusgalli</i>	4.1	4.1	None. (In higher, drier part of same depression).
<i>Amorpha fruticosa</i> , <i>Solidago</i>	6.0	3.5	Nearly barren, few <i>Cassia</i> .
<i>Polygonum</i> , <i>Echinochloa crusgalli</i>	4.2	4.0	None.
<i>Cassia</i>	5.0	3.8	None.
<i>Poa pratensis</i>	7.7	4.5	None.
<i>Rhus glabra</i>	6.0	4.0	None.
<i>Cassia</i> , grasses	5.0	4.0	None.
<i>Melilotus alba</i>	7.3	5.5	Scattered weeds.
Blackberry (<i>Rubus sp.</i>)	5.2	4.0	None.
<i>Poa pratensis</i>	7.0	3.7	None.
<i>Rubus villosus</i> , <i>Poa pratensis</i> (short)	4.5	3.7	None.
<i>Poa pratensis</i> (seedling, 1 inch high)	6.8	3.5	None.
<i>Fragaria virginiana</i> , Violets	5.2	3.5	None.
Blackberry (<i>Rubus sp.</i>)	5.0	3.7	None.
<i>Poa pratensis</i>	6.5	3.7	None.
<i>Melilotus alba</i>	7.3	3.8	None.
<i>Poa pratensis</i>	5.3	4.5	Few short, sickly <i>Poa pratensis</i> plants.
<i>Echinochloa</i> , <i>Carex</i>	6.3	5.2	Few scattered weeds.
<i>Melilotus alba</i> , <i>Helianthus decapetalus</i>	8.0	4.0	None.
<i>Melilotus alba</i> , <i>Helianthus decapetalus</i>	7.5	4.0	None.
<i>Melilotus alba</i>	7.7	4.3	None.
<i>Melilotus alba</i>	7.5	4.5	None.
<i>Melilotus alba</i> (six inches high)	6.7	4.3	None.
<i>Melilotus alba</i>	6.7	5.0	None.
<i>Poa pratensis</i>	7.0	3.5	None.
<i>Sambucus canadensis</i> , <i>Melilotus alba</i>	7.5	4.0	None.
<i>Melilotus alba</i>	7.5	6.5	Few <i>Melilotus alba</i> plants.
<i>Cornus amomum</i> , Cinquefoil	5.3	4.0	None.
<i>Rhus Toxicodendron</i> , <i>Fragaria virgini-</i> <i>ana</i>	7.0	3.8	None.
<i>Brassica nigra</i>	6.5	4.0	None.
<i>Rosa</i> , <i>Fragaria virginiana</i>	7.0	3.8	None.
<i>Solidago</i> , <i>Rosa</i>	5.0	3.8	None.
<i>Melilotus alba</i>	7.0	4.0	None.
<i>Melilotus alba</i>	6.5	3.5	None.
<i>Melilotus alba</i> , <i>Brassica nigra</i>	7.0	4.5	None.
<i>Poa pratensis</i>	6.7	4.2	None.
<i>Rosa</i>	6.7	3.5	None.
<i>Rubus villosus</i>	5.5	3.9	None.
<i>Rosa</i> , Blackberry (<i>Rubus sp.</i>), <i>Melilotus</i> <i>alba</i>	8.0	3.8	None.
<i>Melilotus alba</i> , Blackberry (<i>Rubus sp.</i>), <i>Rhus glabra</i>	8.0	3.6	None.
<i>Helianthus decapetalus</i> , <i>Melilotus alba</i>	7.5	4.0	None.
<i>Solidago</i> , <i>Melilotus alba</i>	6.8	4.0	None.
<i>Melilotus alba</i> (small), <i>Pastinaca sativa</i>	7.0	3.5	None.
<i>Rubus occidentalis</i>	6.0	3.5	None.

Numerous similar determinations were later made throughout the strip-ping fields of the state. The bare spots have a consistently lower pH than adjacent vegetated areas, the average difference being approximately 2.5 pH. The nearly neutral soils are shown to be generally vegetated, while the very acid soils are practically barren. The most acid areas are clearly outlined in the vegetation. The general agreement of these data leaves little doubt of the correctness of the hypothesis that the distribution of the vegetation is closely correlated with the hydrogen ion concentration of the surface soil material.

SOIL MOISTURE RELATION

While the acid determines in large measure the areas where vegetation can thrive, it does not alone explain the data in Table I. The two tests at each location were generally less than four feet apart. When these data are considered without reference to adjacency, the influence of other factors is more clearly seen. An area with a pH of 5.0 may be barren, while another of pH 4.0 or even 3.5 may bear some vegetation. Various observations seem to indicate that water is the other factor of major importance. For example, in the seventh area listed in Table I, the moist depression bore a heavy stand of short *Polygonum* and grasses, while the higher drier ground with the same pH (4.1) remained barren. Likewise it was frequently noted that the vegetation is most luxuriant in the moist portions of areas throughout which the soil reaction is nearly constant. In many of the acid areas, the vegetation dries up quickly on the approach of the dry period. In a few instances high, dry ridges produce little vegetation although they give a nearly neutral reaction. These data and observations show the importance of the water balance directly and in relation to acidity. It is evident from many observations that under moisture conditions favorable for growth the effects of the acid are less, and that they become acute with water shortage.

On some of the steepest slopes erosion is so rapid as to almost completely prevent the growth of plants, and it was the author's first impression that the ridges consisting largely of shale are also rather pervious. This is far from true as was shown by the following experiments. Vertical holes about one foot deep and four inches in diameter were dug in the ridges, care being used not to disturb the surrounding soil. These were then filled to the top with water, and the time required for the disappearance of the water noted. On the basis of preliminary tests an arbitrary scale was devised and used for classifying soils as to their permeability. The results are shown in Table II.

TABLE II. *Classification of stripland soils on the basis of permeability*

Permeable	Fairly permeable	Highly impermeable
(Holes empty after 15 minutes.)	(Holes empty after 1 hour.)	(Little loss of water in 1 hour.)
Soils with a pH of 5.0 or higher.	Soils with a pH of 4.0-5.0.	Soils below pH 4.0.

The results show that the acid ridges are also highly impermeable to water, and would absorb little of the rainfall except in the depressions where the water stands for long periods of time. This factor is probably of very great importance in determining the failure of vegetation.

Early in the study an attempt was made to determine whether the ridges dry out rapidly after being thrown up. An area was selected in Vermilion County representing three successive years of stripping in which the ridges gave the appearance of rather unusually uniform consistency, and soil samples were collected July 20, 1925. The samples were taken half way up the ridges at a depth of six inches, placed in soil cans, and dried at oven temperature. The results are shown below.

TABLE III. *Per cent of soil moisture in ridges of various ages*

Stripped	Collected	Per cent of moisture
July 18, 1925	July 20, 1925	12.8
June 20, 1925	July 20, 1925	13.9
March, 1925	July 20, 1925	15.6
1924	July 20, 1925	9.9
1923	July 20, 1925	9.5

These figures might mean that the old ridges have become less permeable, since they were exposed to all the spring rains in 1925, or it may be only a measure of the water content of the strata at the time of stripping. The progressive order of the figures would tend to bear out the former conclusion. On account of the great heterogeneity of stripland soil material it would require extensive data to establish this fact conclusively. Study of the same ridges at various intervals over long periods of time is likewise attended with great limitations on account of the enormous fluctuations with precipitation.

Numerous edaphic factors, such as direction and slope of the ridges, operate largely through the water relations of the plants. The whole problem of the water balance on stripland soils is so complex that it has been impossible to do more than make a beginning along this line in the scope of the present work.

FERTILITY OF STRIPLAND SOIL MATERIAL

The surface material can hardly be called soil. No definite profile is yet established, and the humus content is very low. The luxuriant vegetation of the neutral and slightly alkaline areas seems to indicate no lack of the necessary plant nutrients. This growth, however, is not evidence of the fertility of the bare areas. One might expect that the subsoil, till, and shale would contain sufficient quantities of the mineral nutrients; but it seemed desirable to test this fact by chemical analyses, although the application of the data is exceedingly limited on account of the great variability in the spill banks.

One composite soil sample was taken from a large bare area and another from a part of the same field occupied by a heavy growth of blue grass and

sweet clover. The prominence of legumes among the plants which are coming in on stripland soils suggested the possibility of nitrogen starvation. It was noted that *Cassia chamaecrista* *Amorpha fruticosa* and other legumes bear a very large number of nodules. Accordingly, a third composite sample was taken from an area in which *Cassia* is prominent. About fifteen pounds of the surface soil material (to a depth of six inches) was secured in each case. This was air dried, pulverized, and the material retained which passed through a ten mesh sieve. Each sample was carefully mixed and a portion was then ground to 100 mesh size. Determinations of total nitrogen,* phosphorous, and potassium were run in triplicate by the usual standard methods of analysis.

The values from these determinations, calculated on a water free basis, appear in Table IV. The results are expressed in terms of the number of pounds per acre (2,000,000 pounds).

TABLE IV. *Total nitrogen (other than nitrate nitrogen), phosphorus and potassium in some stripland surface soil material*

	Highly acid bare soils	Soils on which <i>Cassia</i> is encroaching	Soils bearing sweet clover and blue grass
Nitrogen.....	2,066	1,386	2,000
Phosphorus.....	1,500	1,310	1,216
Potassium.....	41,330	35,000	36,830

It is interesting to note that the barren soil showed a higher content of all three elements than the vegetated soils. Absence of these elements cannot, therefore, account for the failure of vegetation, although the nitrogen content as might be expected is not high. The phosphorus and potassium contents are as great as in most fertile loams. The soils on which legumes are encroaching are shown to contain only about two thirds as much nitrogen as the other samples, but it does not necessarily follow that this fact is significant in their dominance. The deciding factor is the availability and not the total content of the nutrient elements.

A salt well was reported by one of the older inhabitants of the region to have been located a short distance from where the soil samples for analysis were taken. It was thought possible that sodium chloride and the sulphates formed after the pyrite oxidation might have resulted in such a high total concentration of water soluble salts as to render the plants unable to absorb the water. To test this hypothesis the total salts were determined in clear soil solution extracts obtained by dialysis through collodion bags, somewhat according to the manner recently described by Pierre and Parker ('27).

* Nitrate nitrogen forms a small, but exceedingly variable fraction of the total nitrogen, its variation throughout the year being so great as to render its determination of little value during the late fall when these samples were taken.

TABLE V. *Total water soluble salts in some stripland soils*

Highly acid bare soils	Soils on which <i>Cassia</i> is encroaching	Soils bearing sweet clover and blue grass
.737%	.033%	.059%

The total water soluble salt content is seen to be much above that of agricultural soils of the region, yet well below the point where plasmolysis might be expected to take place. The greatest amount, as in the case of sulphur (Table VII), was obtained from the highly acid soils. It seems possible that the additional soluble salts may be largely soluble sulphates.

While the total amount of salts is not sufficient to prevent the plants from obtaining water, it is possible that sodium liberated through exchange effected by the hydrogen ions might account for the impermeability of these highly acid soils. If this be true it is not due to the presence of sodium from salt wells, since such highly acid soils are generally impermeable throughout the striplands.

One would expect replacement of exchangeable bases by hydrogen ions to be an item of considerable importance in the fertility of stripland soils. The work of Kelly and Brown ('26) and others indicates that in some acid soils this replacement of bases and the subsequent leaching may result in the removal of nearly all of the available base supply. It is frequently impossible to obtain an indication of calcium in the water extract of such soils. However, when these highly acid stripland soils were leached with water, calcium was present in the water extract in the proportion of 5,000 pounds per acre (2,000,000 pounds of soil). The calcium obtained by extraction with a N/10 solution of KCl was 4,560 pounds per acre in this same sample and 2,500 pounds in another sample obtained from one of these impervious acid areas. Analysis of the latter showed this to be approximately two thirds of the total amount of calcium present in the soil. Stephenson ('26), who studied the oxidation of sulphur in soils, found the total amount of water soluble calcium to be a rather sensitive indicator of the amount of sulphur oxidized. Large amounts of exchangeable magnesium⁴ were also shown to be present, 6,900 pounds per acre in the water extract and 6,550 pounds by replacement with KCl.

The entire subject of base exchange is still in an early stage of development. Moreover the data here are exceedingly limited, and this phase of the problem of the fertility of stripland soils alone would constitute an extensive study. The results obtained, however, suggest two meanings. The large amount of exchangeable bases present is probably a characteristic of youthful soils, the material having had a relatively short period in which to be leached away in comparison with the long period of leaching to which

⁴ For the determination of total and exchangeable Ca and Mg, I am indebted to M. P. Catherwood and F. H. Crane of the staff in soil fertility at the University of Illinois.

our agricultural soils of the region have been subjected. Secondly these results are in accord with what might be expected from the high degree of impermeability of these acid stripland soils. In permeable soils the bases tend to be leached away as they are released into the soil solution. In these impermeable soils their removal is retarded, and they tend to accumulate. The exchange has progressed to such a degree, however, as to be a probable factor of considerable importance in the eventual fertility of these soils.

With the hope of throwing some light on the availability of the nutrient elements and of checking the hypothesis that the failure of plants is due in large measure to the acidity, some experiments were undertaken in which plantings were made in these soils both in place and transferred to six inch flower pots where adequate moisture could be supplied. The data are somewhat lengthy and there is only space here to indicate the most significant results. No growth was obtained on the most acid soils without treatment. When sufficient ground limestone was added to render the reaction neutral, wheat made excellent growth which was not appreciably increased by the addition of nitrogen, phosphorus, and potash fertilizers. Similar results were obtained with soybeans, red clover, and sunflowers (*Helianthus annuus*). Neutral soils gave excellent results, and some growth occurred on soils with a pH of 4.3. The failure to obtain marked stimulation by the addition of nitrogen is perhaps the most surprising result obtained, although Stephenson ('20), who has studied nitrification in soils rendered acid with H_2SO_4 , has shown that a loam soil with a lime requirement of twelve tons per acre may contain a considerable amount of nitrates. It is not possible to state in what manner $CaCO_3$ renders these soils productive. From the high degree of productivity of the neutral areas, the good growth obtained by liming and the failure to obtain marked stimulation by the further addition of fertilizers, it seems reasonable to conclude that these soils are not necessarily infertile if proper conditions for plant growth be established, probably the most important of which is a lower hydrogen ion concentration.

Striking results were obtained by analyzing the soils for their sulphur content, as shown in Table VI.

TABLE VI. *Sulphur content of three composite stripland soil samples. (Results in pounds per acre)*

Highly acid bare soils	Soils on which <i>Cassia</i> is encroaching	Soils bearing sweet clover and blue grass
33,240	2,640	834

The differences in sulphur content are much greater than those of the other elements studied, and furnish another point of indirect evidence that this factor is more important than any lack in the total amounts of the nutrient elements.

TREND OF SUCCESSION ON COAL STRIPPED LANDS

A series of markers was placed on some of the newly formed ridges as a means of studying the beginnings of vegetation and the later successions. Under favorable conditions plants appear within a few days after the formation of the ridges. Probably most prominent among these earliest appearing plants are the bindweeds, *Convolvulus sepium* and *C. arvense*, the little morning glory, *Ipomea hederacea* and some of the grasses, especially *Setaria*; although a large number of species were collected on the recently formed ridges. The appearance of many of these plants was such as to mark them as vegetative shoots rather than very young seedlings, and this hypothesis was readily confirmed in many cases by digging down along the shoots to determine their origin. Extended observations on the newly formed ridges have confirmed the fact that many of the first plants to appear have their origin in buried plant parts.

The small part of the vegetation which survives the stripping process is augmented by large numbers of pioneers arising from seeds during the periods favorable for germination. Most species are unable to endure the extreme conditions. Many others, while seemingly unable to spread over the ridges, exist as solitary individuals or as small colonies. Among the more successful invading species which form larger colonies, the most commonly encountered are *Polygonum pennsylvanicum*, *Convolvulus sepium*, *Convolvulus arvense*, *Ipomea hederacea*, *Helianthus decapetalus*, *Lactuca scariola*, *Lactuca canadensis*, *Ambrosia trifida*, *Ambrosia artemisiifolia*, *Ambrosia bidentata* (southern Illinois), *Melilotus alba*, *Brassica nigra*, *Solidago* sp., *Setaria glauca*, *Setaria viridis*, *Oenothera biennis*, *Rumex acetosella*, *Tacoma radicans*, *Typha latifolia* (in swamps), *Xanthium commune*, and *Echinochloa crusgalli*, the last two mainly along the borders of ponds and drainways.

Except where revegetation is delayed by high hydrogen ion concentration or extreme exposure, these scattered communities are soon brought into contiguity by the rapid spread of one or more species. This usually occurs within the first year or two, and may take place within the first few weeks after the spill banks are formed. This closing of ranks is so generally accomplished by *Polygonum pennsylvanicum* that the period may properly be called the smartweed stage in stripland succession. *Polygonum pennsylvanicum* endures a wide range of moisture conditions and seems to grow almost equally well in medium acid, neutral, and slightly alkaline soils. It is so universally abundant throughout the stripping fields of the state that the young ridges may usually be identified, even at a distance by the characteristic aspect it presents.

Usually within two or three years *Melilotus alba* begins to appear among the smartweeds. Within five years it is dominant over large areas, although it seems to be restricted to soils which are not acid. It is slower to appear in the southern Illinois fields, possibly on account of scarcity of seed plants

in the surrounding territory. There the smartweed stage is frequently replaced by a mixed weed flora in which the wild lettuces are prominent. Where sweet clover is once established it holds unquestioned sway as the dominant species. It makes a heavy growth on the limy soils, attaining a height of six or seven feet, and adding much needed organic matter to the soil.

In many places the woody plants gained a foothold with the ruderals, and are developing in open stands along with the sweet clover. In others they are now coming in; but nowhere have they developed into forest on the spill banks, although the stand is nearly closed in a few places. It is impossible at present to state how long it will be before the tree stand is entirely closed and forest conditions established. The trees are mostly quick growing types, *Populus deltoides* and *Platanus occidentalis* being far the most abundant species. *Acer saccharinum* has appeared in large numbers on the Fulton County stripped land, and *Ulmus americana* and the green ash, *Fraxinus pennsylvanica* variety *lanceolata*, occur in limited numbers in restricted areas in several fields. In the fields of southern Illinois, the persimmon, *Diospyros virginiana*, is common. The willows form margins around the ponds or thickets in the moist areas of all stripped lands in the state.

The Illinois striplands lie mainly in the transitional belt between forest and prairie, and small areas of natural forest are present in the vicinity of each spill bank area. The climate is, of course, less favorable for forest development than it is farther to the East, and the successional period is therefore considerably longer. Ultimately, however, they may be expected to develop into climax forest if undisturbed.

At various places where the coal has been removed along Salt Fork Creek in Vermilion County, well developed bottomland forests now exist. One of these areas was studied by McDougall ('18a, '25), who called attention to the rapidly developing forests. Certain observations during the course of the present study have indicated that the development on this area is hardly to be considered as stripland succession. The water of Salt Fork stream was found to have an alkaline reaction, as does the water standing in the depressions in these bottomland forests. The drainage of some of these areas was traced out, and the areas likely to be flooded were found to correlate rather closely with those now occupied by forests. The flooding of these tracts by backwater from the stream was verified during the flood stage in September, 1926, which lasted several days. A deposit of alluvium of varying thickness, averaging probably a half inch, was left over this area. The surface soil showed an alkaline reaction and effervesced violently with hydrochloric acid for a considerable distance back from the stream. Borings were made at a number of points to determine the depth of the alluvium layer and the neutralization effects of the alkaline material and stream water. The results are shown in Table VII.

TABLE VII. Showing results in pH values obtained by borings in the forest region along Salt Fork Creek in Vermilion County

Depth inches	A	B	C	D	E	F	G
0	7.5	8.0	7.7	7.5	7.5	7.7	8.0
6	8.0	8.0	8.0	7.5	7.5	7.5	8.0
12	8.0	8.2	7.7	7.5	7.5	7.5	8.0
18	7.5	8.2	7.6	7.5	7.5	7.5	8.0
24	7.5	7.8	7.6	7.5	7.5	7.5	8.0
30	7.7	7.8	7.7	7.5	7.5	7.5	8.0
36	8.0	7.8	7.6	7.5	7.5	7.5	8.0
42	7.5		7.7	7.5	7.3	7.5	4.0*
48			7.5			7.5	7.0
54			7.3			7.5	
60			7.5			7.5	
66			7.5			7.5	
72						7.5	
78						7.5	

A, B, and C on the low ridges.

D, E, and F in the troughs.

G on nearly level area near the stream.

Alluvium above the dotted line, spill banks below.

* Later tested 7.5 at a distance of 18 inches from first hole.

Study of the alluvium at other points indicated that it varies in depth from a few inches to many feet over this area. The forest is growing upon this alluvial soil deposited by the stream on top of spill banks. Although the roots probably penetrate the stripland soil material, its acidity has been corrected, except immediately about the pyrite lenses, and doubtless much added to its fertility by the stream water and leaching of the overlying alluvium. These areas are, moreover, much better supplied with water than other stripland soils. The rapid development of forests under these conditions cannot, therefore, be taken as any indication of the rate of succession on striplands unaltered in this manner.

In this discussion of the trend of succession, attention has thus far been directed mainly toward the neutral and slightly alkaline areas. The soils of probably half of the stripped areas are acid, calcareous strata having been lacking in the overburden or insufficient to neutralize the acid liberated by oxidizing pyrites. Where the hydrogen ion concentration is not greater than pH 5.0 or even 4.5 the revegetation is progressing, provided conditions are otherwise not too unfavorable. The ruderal communities are less numerous, but the smartweed stage makes its appearance in about the same length of time and holds even more unbroken sway, since *Helianthus decapetalus*, *Ambrosia trifida*, and certain other of the more hardy pioneers of the limy soils are lacking. While it is true that *Ambrosia artemisiifolia* (and *A. bidentata* in the southern fields), *Rumex acetosella*, *Cassia chamaecrista*

and other of the acid tolerant plants are more in evidence, the smartweed stand is less broken by other ruderal communities, although the plants are farther apart. The sweet clover stage is entirely lacking and no records of the growth of sweet clover on markedly acid soils were obtained. The smartweeds are to some extent eventually replaced by a mixed stand of annual and perennial weeds, and this stage is apparently continuing while the acid tolerant cottonwoods and sycamores (also persimmon in the southern fields) are coming in. In one of the older stripped areas in Williamson County the cottonwoods, while in open stand, have reached a considerable size. The herbaceous vegetation, however, is apparently still in the ruderal stages. It seems altogether likely that forest will be developed on this land without distinct intervening herbaceous stages. There is much telescoping of stages in stripland successions, and the problem from a successional standpoint is exceedingly complex. There is much evidence, especially on the acid soils, to indicate that succession here is largely allogenic and not phytogenic; but the problem as to the extent of each agency here, as elsewhere, remains to be solved.

It will probably have been noted that no mention has been made in this discussion of a shrub stage in the successions. Isolated communities of *Rubus occidentalis*, *Rubus villosus*, two or more species of blackberries, *Rhus glabra*, *Sambucus canadensis*, *Symphoricarpus orbiculatus*, *Cornus amomum*, *Amorpha fruticosa*, *Tacoma radicans*, various species of wild grapes and other of the small woody plants are a rather conspicuous feature of stripland vegetation. While they are, of course, able to maintain themselves against the encroachment of herbaceous species, they give little evidence of ability to spread over the surrounding areas. They generally occupy only a few square yards or at most a few square rods and are to be regarded as representing smaller communities within the larger areas rather than a stage in the general succession. A possible exception to this statement is found on an acid portion of the bottomland strippings in Vermilion County where *Amorpha fruticosa* seems to be succeeding a *Cassia* and *Fragaria* stage over an area a few acres in extent.

Very little study of the hydrophytic successions of the stripland region has been undertaken, although examples are numerous and interesting. Many of the ponds are deep, the water reaching a depth of thirty-five feet in some, and the sides are very steep. The depressions are slow to fill and only the shallower ponds show marked successional progress. There is little evidence that the hydrophytic successions are of great importance in developing mesophytic vegetation. Indirectly through their influence on the habitat they are doubtless of considerable importance. In some cases the moist depressions probably act as centers of distribution aiding in the spread of plants to surrounding ridges.

RETARDATION OF VEGETATION ON HIGHLY ACID AREAS

At various places in this discussion attention has been called to the highly acid areas which remain barren. One wonders how long the revegetation of these areas will be prevented or retarded. Collection and tests of the run off from the highly acid ridges proved that acid is leached from the surface during heavy rains. Borings made in these areas showed that the high hydrogen ion concentration is maintained even to a depth of five and one half feet, being only slightly lessened at the surface. The surface soil is practically neutralized along the margins of the bare areas and where isolated patches of vegetation occur in the midst of an otherwise bare area.

It was shown (Table II) that the vegetated soils are readily permeable, water sinking quickly into the soil. Even soils with a pH as low as 4.0 were shown to be fairly permeable, while the most acid soils were highly impermeable. In the light of these data the reason for the long continued high hydrogen ion concentration and consequent failure to revegetate may readily be seen. Very little rainfall penetrates the most acid ridges, and that to a very short depth. While acid is leached from the surface and carried away in the run off, the process affects the ridge to no great depth. This leaching is accompanied by an erosion effect and leaves little acid free material behind, but is continually lowering the ridge by removal of the surface material. The two processes probably keep nearly apace for a time, each year new material being exposed as the surface of the ridge is leached and eroded away. As the ridges become older their sides are less steep and erosion consequently slower. It would seem that penetration of the water should for the same reason be increased, and the lessening of the acidity be accomplished. This seems to be what is now gradually taking place, the soil material which was more permeable at the outset being much more advanced in the leaching process. These highly acid bare spots may, therefore, be expected to revegetate eventually; although it is difficult to predict how long the process will take. In places there has been little progress other than the lowering of the ridges, although acid has been leached away by the rains of nearly half a century.

SUMMARY.

With the present rapid expansion of the coal stripping industry, valuable agricultural lands in various parts of Illinois are being disturbed, the strata overlying the coal being left in the form of parallel ridges known as "spill banks" or "waste banks."

Differences in the overburden, especially in the amount of calcareous and shaly material, and irregularity in the action of the stripping shovels result in great variability in the material composing the waste banks.

The oxidation of the iron pyrites from the waste coal and overlying shale liberates sulphuric acid in the ridges, and results in a high hydrogen ion concentration of the soil in innumerable irregular areas.

In probably half of the stripped areas the calcareous material of the overburden renders the spill banks neutral to slightly alkaline.

The distribution of the present vegetation of the stripped areas is closely correlated with the hydrogen ion concentration of the surface soil material. The nearly neutral soils are generally heavily vegetated. Vegetation tends to become well established under favorable conditions above pH 4.5, and generally fails below that point. The acid areas are clearly outlined in the vegetation.

The effect of water and other factors can be seen in the variations in the vegetation at any given pH.

The material of the spill banks has hardly developed to a stage where it may properly be called soil, and no definite horizons are yet distinguishable. It is low in organic matter. Although the nitrogen content is not high, there is little indication either from analysis or from growth experiments that the unproductivity of the bare areas is due to deficiency in the supply of nutrient elements. When limed, these soils produce well.

The first plants to appear on the ridges generally arise from buried plant parts. These are followed by large numbers of individuals of many species arising from seeds. The stand is usually closed by the rapid spread of *Polygonum pennsylvanicum*. Within two to five years *Melilotus alba* replaces *Polygonum pennsylvanicum* on the neutral and slightly alkaline areas and holds unquestioned dominance. Many of the smaller woody plants and a few species of trees, especially *Populus deltoides* and *Platanus occidentalis*, have gained a foothold along with the ruderals, and are now developing among the sweet clover plants. The tree stand is slowly closing.

On the medium acid soils the *Polygonum* stage maintains itself for a longer period. On some acid areas the herbaceous vegetation has never developed beyond the ruderal stage, although the cottonwoods have reached considerable size. It seems clear that plant succession on the acid areas is largely allogenic rather than phytogenic.

On the most acid areas of the earliest strippings, revegetation has already been prevented for a long period and can take place only when the hydrogen ion concentration is lessened. The water soluble sulphuric acid is leached from the surface of the ridges by the rains. These areas are generally highly impermeable to water, however, and the water erodes the surface away as it is leached, exposing ever fresh, unleached, highly acid soil. The ridges are gradually lowered by this process and the penetration increased while the erosion is decreased. The surface material will, therefore, in time be sufficiently freed from acid for revegetation to take place.

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PHYSICAL CHARACTERISTICS AND SILVICULTURAL IMPORTANCE OF PODSOL SOIL

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INTRODUCTION

Forestry and agriculture have much in common. The crop production of plant life in various forms is the primary object of both sciences. In no way is the common relationship between forestry and agriculture more fully demonstrated than by the dependence of their crops upon the condition and health of the soil for existence and growth.

Although forest soil science can be said to have been initiated in 1893 when Ramann published his masterly work on "Forstliche Bodenkunde und Standortshhre," it has not kept pace with similar developments in agricultural soil science. The catastrophies which in recent years have overtaken spruce forests in Saxony have stimulated the interest in forest soil studies. The resulting decrease in site quality has manifested the need for a more rational use of forest soil. In Saxony, since 1850 (Anonymous, '23), forest management has been based chiefly upon a financial rotation, no effort being made to maintain the soil fertility through the introduction of hardwood species. Clear-cutting and replanting of pure Norway spruce have been the outstanding features of the system, and until recently the results apparently have been excellent. However, at present the annual cut is but 40 cubic feet per acre, whereas before the war it was 69 cubic feet. This represents a falling off in yearly growth of almost 45 per cent. Among the several reasons alleged for this reduction is the development of podsol soil, a soil formation characteristic only of wooded land. In Saxony, it was found (Anonymous, '23) that "pure stands of spruce fail to maintain the fertility of the soil. The soil loses its life; *it turns a blue-gray color*;" there are no rainworms, no microbes, no insects in it; it is littered by a sort of peat 'Trockentorf,' which seems to cover the soil in an air-proof and moisture-proof layer. During the first generation of pure spruce, these changes and these drawbacks do not seem to enter an appearance. In the second and third, they become evident, particularly during dry seasons. The result is utter stagnation of growth." In the words of Dr. C. A. Schenck, the forest soils of Saxony are "sick," and their former productiveness can be restored only after many years of careful work.

THE PODSOL SOIL PROFILE

The term podsol or podzol, as it is more correctly spelled, is of Russian derivation. It is synonymous with the German "Grauerde," "Bleicherde,"

or "Aschenerde," and means ash- or cinder-colored. The term describes very appropriately the degenerated forest soil in which the characteristic leached-out gray horizon has been formed. Originally, the term podsol applied more specifically to the gray-colored zone, though now it is commonly used to describe the entire profile or any process or processes which culminate in lowering the soil quality.

In general it can be said that podsol soils occur under two very distinct conditions: first as the result of the natural environmental factors, and secondly where the forest produces conditions favoring the podsol process. In the former case, the presence of this soil type may or may not indicate poor soil conditions. In the latter, it does show that serious harmful changes have taken place in the soil. Thus for example, as Hesselmann ('25) points out, while a soil type with raw humus and leached soil is normal for Swedish forests, such conditions in Middle Europe are regarded as signs of the beginning of degeneration. Where the podsol process is simply a part of the natural environment, as is the case with the Cherry Mountain soils, such soils may have humus in the form of "northern mull" and not in the raw state. Notwithstanding the podsol formation found under such humus, this soil can be considered favorable for that particular climatic region.

European forest soil literature contains numerous references to podsol soil. Ramann ('11) gives an excellent description of its formation and distribution in Europe. Glinka ('24) and Niklas ('24) have both investigated the podsol formation in Russia. Recently Hesselman ('25), in his prodigious research on humus layers in coniferous forests and their dependence upon silviculture, has described it as found in Sweden and Germany. In this country McCool, Veatch, and Spurway ('23), in their soil profile studies in Michigan, distinguished and reported the gray forest soil common to the northern part of the peninsula as contrasted with the brown soil found farther south. Bray ('15) has found the leached soil very common to the sand beds of the Adirondack Mountains in New York. Edgington and Adams ('25) have worked on the nitrogen distribution of samples taken from a podsol profile at Cherry Mountain, New Hampshire.

Ramann ('11) limits the boundaries of the podsol soil distribution in Europe to the regions of cool temperatures where there is abundant rainfall and severe winters. In the United States it is generally believed that this soil formation is coexistent with the spruce-fir-northern hardwood region of the Northeast and Lake States—a region of humid climate and other climatic conditions similar to those outlined by Ramann. It is found also in the white pine region of New England, but in a much less clearly defined area. Probably this soil type extends north through the wooded areas of northeastern Canada. Podsol soil can likewise result, as has been previously mentioned, from a one-sided silvicultural system which produces pure stands, especially of conifers. This will be discussed at some length later.

PHYSIOGNOMY AND FLORISTIC COMPOSITION OF THE CHERRY MOUNTAIN FORESTS

During the late summer and early fall of 1924, the Northeastern Forest Experiment Station established a series of permanent sample plots at Cherry Mountain, New Hampshire. The forests in the vicinity of the plots are typical stands of mixed spruce-fir-northern hardwoods. The area has good drainage conditions, moderate to steep slopes, and a general east to southeast exposure. The overwood, though mature and presenting a virgin forest appearance, was lightly culled for large spruce timbers some fifty years ago. At the time the plots were established, the dominant red spruce trees had reached an age of between 180 and 250 years. The tallest tree on the plots, a red spruce, had a height of 83 feet with a diameter at breast height of 20.7 inches. The diameters of the species at breast height varied from 1 inch to 26 inches. A tally of all trees one inch and over in diameter on a half-acre plot gave the following distribution per acre:

TABLE I. *Percentage distribution and basal area of tree species per acre*

Species	Number	Percentage	Basal Area*	Percentage
Red spruce (<i>Picea rubens</i>).....	162	35.8	62.730	41.71
Balsam fir (<i>Abies balsamea</i>).....	76	16.8	13.026	8.66
Yellow birch (<i>Betula lutea</i>).....	138	30.5	58.812	39.11
Sugar maple (<i>Acer saccharum</i>).....	6	1.4	5.372	3.57
Beech (<i>Fagus grandifolia</i>).....	26	5.8	5.814	3.87
Others †.....	44	9.7	4.636	3.08
Per acre.....	452	100.0	150.390	100.0

* Basal area is the area section of a tree, usually expressed in square feet, and usually referring to the section at breast height. The sum of the basal areas of trees in a stand is the basal area of the stand and is usually expressed in square feet per acre.

† Others comprised the following species—red maple (*Acer rubrum*), striped maple (*Acer pennsylvanicum*), mountain maple (*Acer spicatum*), and pin cherry (*Prunus pennsylvanica*).

The underwood and herbaceous growth, as is typical of our northern mixed softwood-hardwood forests, was very prolific both in number of species and area distribution. It consisted for the most part of sapling and seedling growth of overwood species with a preponderance of the three maples—red, mountain, and striped—pin cherry, and witch hobble (*Viburnum alnifolium*).

The frequency distribution of herbaceous growth was as follows:

TABLE II. *Distribution of herbaceous growth*

ABUNDANT	COMMON
Witch Hobble (<i>Viburnum alnifolium</i>)	Star Flower (<i>Trientalis americana</i>)
Clintonia (<i>Clintonia borealis</i>)	Twisted-stalk (<i>Streptopus amplexifolius</i>)
Wood Sorrel (<i>Oxalis Acetosella</i>)	Miterwort (<i>Mitella nuda</i>)
Wild Sarsaparilla (<i>Aralia nudicaulis</i>)	False Miterwort (<i>Tiarella cordifolia</i>)
Bunchberry (<i>Cornus canadensis</i>)	Violet (<i>Viola</i> sp.)
Canadian Mayflower (<i>Maianthemum canadense</i>)	Indian Pipe (<i>Monotropa uniflora</i>)
Aster (<i>Aster acuminatus</i>)	SCARCE
Spiney-shield Fern (<i>Aspidium spinulosum</i>)	Rattlesnake Plantain (<i>Epipactis pubescens</i>)
Common Club Moss (<i>Lycopodium clavatum</i>)	White Trillium (<i>Trillium erectum</i>)
Groundpine (<i>Lycopodium complanatum</i> var. <i>flabelliforme</i>)	Painted Trillium (<i>Trillium undulatum</i>)
<i>Lycopodium lucidulum</i>	Orchis (<i>Habenaria</i> sp.)
<i>Lycopodium obscurum</i> var. <i>dendroideum</i>	Sweet-scented Bedstraw (<i>Galium triflorum</i>)
	Rough Bedstraw (<i>Galium asprellum</i>)
	Dwarf Raspberry (<i>Rubus triflorus</i>)

PHYSICAL PROPERTIES OF PODSOL SOIL

Excellent examples of strongly leached soil were abundant on the areas selected for the permanent sample plots. The appearance of soil profile is given below (see also Figs. 1 and 2). The numbers represent the average of a series of twelve soil well measurements. The Swedish (Swd.) and German (Ger.) terms are given whenever possible.

A₀—ORGANIC HORIZON.

Horizon of pure organic matter; depth 1.0 to 4.0 inches, with an average of 2.6 inches.

A₀¹—*Litter Zone* [Förnerskiktet (Swd.); Streuschicht (Ger.)]. "The unaltered total dead remains of plants or animals." No decomposition other than weathering is found in this zone, which consists primarily of the more recently fallen leaves, twigs, and small branches. On account of the physical state of the organic matter, aeration is excellent.

A₀²—*Duff Zone* [Förmultningskiktet (Swd.); Vermoderungsschicht (Ger.)]. The region intermediate between the litter zone and the humus zone, and consisting of organic matter in the process of decomposition whose structure is still plainly visible. Aeration is moderately good and fungal hyphae or mycelial threads are generally lacking. This is the so-called F-layer of Hesselman ('25).

A₀³—*Humus Zone* [Humusamneskiktet (Swd.); Humusstoffschicht (Ger.)] "The sum total of organic remains of plants or animals which have become part of the soil and have been therefore subjected to an alteration process." The decomposition in this layer has gone so far that the plant structures are no longer distinguishable. Aeration is very poor, and, where raw humus [Råhumus (Swd.); Rohhumus (Ger.)] is found, the layer is always felt-like and interwoven with fungal hyphae and mycelial threads. This is the layer designated as H by Hesselman.

A—LEACHED HORIZON.

Horizon from which the organic matter and inorganic colloids have been washed out into the next lower horizon, and from which the soil formation derives its name. Depth 0.5 to 7.0 inches; averaging 2.9 inches.

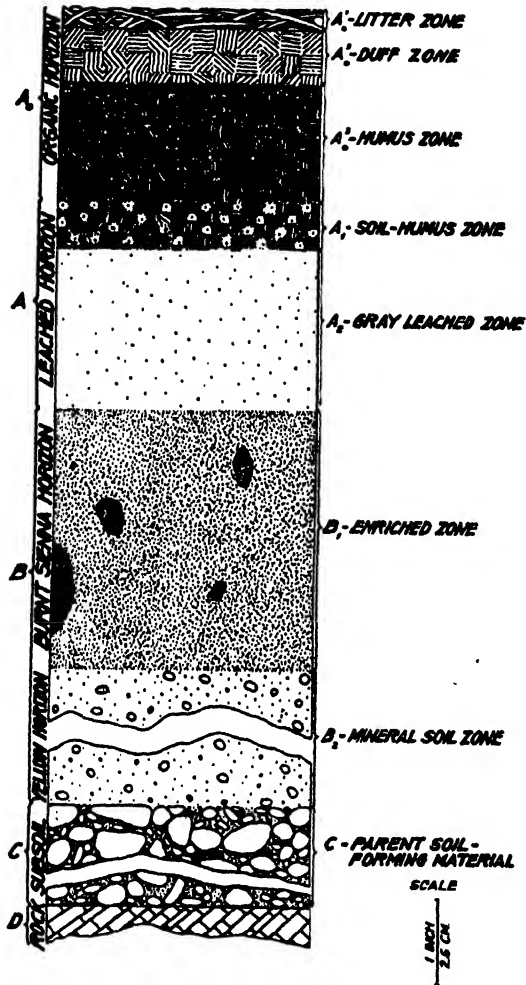


FIG. 1. Profile of podsol horizons at Cherry Mountain, New Hampshire.

A₁—Soil-Humus Zone. A rather thin band of black concentrated admixture of humus and soil; "nut"-like in structure, and characterized by the presence of white quartz flour on the surface of the organic matter. A transition zone between the organic horizon and the leached horizon.*

* This transition zone may be so thin in the undisturbed podsol profile as to be almost indistinct, and in some cases it may be entirely lacking. The soil-humus zone is however very characteristic of the podsol profiles of old pasture spruce stands and of second growth white pine forests.

A₂—Leached Zone [Blekjordskiktet (Swd.); Bleichschicht, Aschenerde or Grauerde (Ger.)]. A zone of almost pure white to blue-gray sand, with scarcity of organic matter.

B—BURNT SIENNA AND YELLOW HORIZONS.

B₁—Burnt Sienna Horizon.

Enriched zone, burnt sienna in color (sometimes spoken of as *coffee brown*). Horizon of rather uniform texture with small concretions of very dark brown to almost black particles. Depth 1.0 to 10.0 inches; averaging 4.0 inches.

B₂—Yellow Horizon.

Mineral soil zone, yellow to rust-colored, in which there is a concentration of iron compounds; depth undetermined.

C—SUBSOIL HORIZON.

Zone of parent, soil-forming materials; glacial origin; depth undetermined.

D—ROCK HORIZON.

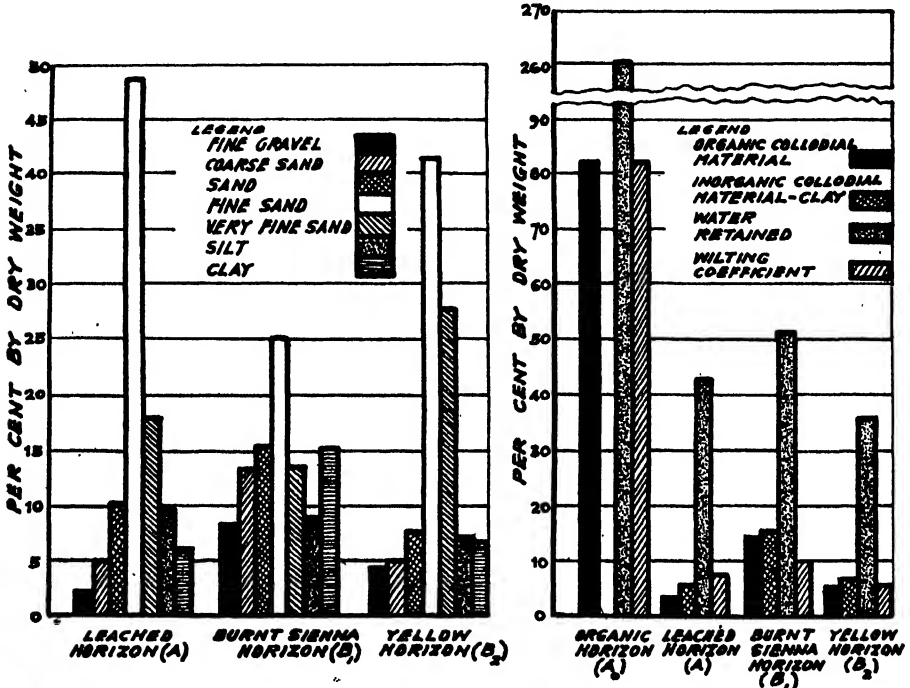
Parent bed-rock; composed mainly of granite and gneiss.



FIG. 2. Soil well in podsol soil at Cherry Mountain, New Hampshire.

It should be remembered that the above terms and definitions are morphological. All of the zones distinguished may or may not be present in every forest soil, depending upon climatic as well as upon forest floor conditions. Thus, for example, in the best type of mull soil, humus is present, but in a

much different quality and quantity than in the less favorable forest soils. In the former, ecological conditions produce rapid oxidation and decomposition of the detritus materials, resulting in a very thin, loose organic horizon. In the latter, on the contrary, the site factors lead to the formation of a dense felt-like layer of organic matter which we term raw humus.



FIGS. 3 AND 4. Fig. 3 (left). Percentages of soil fractions in the various horizons of a podsol profile. Fig. 4 (right). Relationship between the amount of colloidal materials in the horizons of a podsol profile and the retentive capacity for water and the wilting coefficient.

Samples were collected from each of the first four horizons. In the laboratory, specimens of each of the above were subjected to the regular mechanical analyses as used by the Bureau of Soils, the ignition test for estimation of organic matter, and the Hilgard method of determining the maximum water-holding capacity. All tests were done in duplicate. Edgington and Adams ('25), working with samples from these identical horizons, determined the nitrogen content, acidity, and moisture equivalent.

a. Mechanical Analyses of the Horizons

Table III and figure 3 show the percentage of the various soil fractions in the three soil horizons. It was not possible to make such a determination for the humus or soil-humus layers, because of the presence of excessively large amounts of organic matter. Ten-gram samples were used.

TABLE III. *Distribution of soil fractions in horizons of the Cherry Mountain podsol profile*

Separate	Size of particles mm.	Horizons		
		Leached per cent	Burnt sienna per cent	Yellow per cent
Fine gravel.....	2.0 -1.0	2.19	8.34	4.29
Coarse sand.....	1.0 -0.5	5.07	13.26	5.01
Sand.....	0.5 -0.25	10.24	15.62	7.67
Fine sand.....	0.25 -0.10	48.91	25.12	41.39
Very fine sand.....	0.10 -0.05	17.92	13.35	27.76
Silt.....	0.05 -0.005	9.69	8.95	7.23
Clay.....	0.005-0.0001	5.98	15.36	6.65
Totals.....		100.00	100.00	100.00
Classification.....		Fine sand	Sandy loam	Fine Sand

b. Estimation of Organic Matter

Oven-dried samples were placed in heat-resistant crucibles and ignited at a low red heat until all the organic matter had been oxidized. The cold mass was then moistened with ammonium carbonate and reheated to a temperature of approximately 150° C. to drive off all the ammonia and replace the carbon dioxide. When no further loss in weight could be detected, the samples were finally weighed, and the loss in weight was taken as the amount of organic matter present. The results were as follows:

TABLE IV. *Organic matter in horizons of the Cherry Mountain podsol profile*

Horizon	Percentage of organic matter
Organic.....	83.17
Leached.....	2.96
Burnt Sienna.....	15.12
Yellow.....	4.86

c. Maximum Water-Holding Capacity and Wilting Coefficient

The maximum water-holding capacity was determined with the usual perforated brass cup holding a column of soil one centimeter thick in accordance with the Hilgard ('12) method. The wilting coefficient was calculated, using the data in Table V with the formula (Lyon and Buckman, '22):

$$\text{Wilting coefficient} = \frac{\text{water-holding capacity} - 21}{2.9} :$$

TABLE V. *Maximum water-holding capacity and calculated wilting coefficients of horizons of the Cherry Mountain podsol profile*

Horizon	Maximum water-holding capacity Percentage of dry weight of soil	Calculated wilting coefficient
Organic.....	260.69	82.7
Leached.....	43.49	7.8
Burnt Sienna.....	51.90	10.7
Yellow.....	36.00	5.2

The relations between the colloidal materials in these four layers, the amounts of water retained, and the calculated wilting coefficients are graphically presented in figure 4.

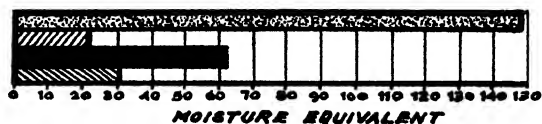


FIG. 5 MOISTURE EQUIVALENT OF THE HORIZONS OF A PODSOL PROFILE (AFTER EDGINGTON AND ADAMS).

LEGEND
SOIL-HUMUS ZONE (A₁)
GRAY LEACHED ZONE (A₂)
BURNT SIENNA HORIZON (B₁)
YELLOW HORIZON (B₂)

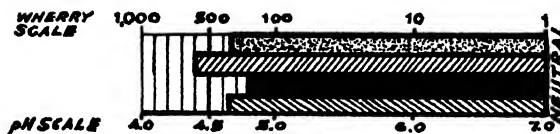


FIG. 6 ACIDITY OF THE HORIZONS OF A PODSOL PROFILE (AFTER EDGINGTON AND ADAMS)

LEGEND
SOIL-HUMUS ZONE (A₁)
GRAY LEACHED ZONE (A₂)
BURNT SIENNA HORIZON (B₁)
YELLOW HORIZON (B₂)

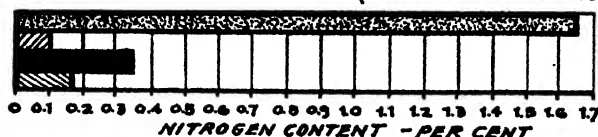


FIG. 7 PERCENTAGE OF NITROGEN IN THE HORIZONS OF A PODSOL PROFILE (AFTER EDGINGTON AND ADAMS)

LEGEND
SOIL-HUMUS ZONE (A₁)
GRAY LEACHED ZONE (A₂)
BURNT SIENNA HORIZON (B₁)
YELLOW HORIZON (B₂)



FIGS. 5, 6 AND 7. See captions under each figure.

d. Moisture Equivalent, Acidity, and Nitrogen Distribution

The determination of the moisture equivalent, acidity, and nitrogen distribution by Edgington and Adams ('25), using samples of the podsol soil from Cherry Mountain, New Hampshire, are presented herewith. The graphical presentation will be found in figures 5, 6, and 7.

TABLE VI. Moisture equivalent, acidity, and nitrogen content of horizons of the Cherry Mountain podsol profile (after Edgington and Adams, '25)

Horizon	Moisture equivalent percentage by dry weight of soil	Acidity pH	Nitrogen content percentage
Soil-Humus.....	148.9	4.66	1.660
Leached.....	21.9	4.40	0.099
Burnt Sienna.....	62.7	4.80	0.348
Yellow.....	30.6	4.65	0.164

e. Chemical Analyses

No chemical determinations, other than for nitrogen and hydrogen ion concentration, were made with samples taken from these profiles. It is of interest to record the findings of Niklas ('24) in this connection. This investigator, working with bleached sand and soil formed in situ (the burnt sienna horizon soil), found that the enriched layer, as contrasted with the leached layer, contained five times as much iron, twice as much aluminum oxide and phosphoric acid, and one and a half times as much soluble silicon oxide. These results agree closely with the work of McCool, Veatch and Spurway ('23), who, in their chemical analyses of the podsol horizons of northern Michigan, found that there was three and a half times as much nitrogen, three times as much iron oxide, two and a half times as much aluminum oxide, twice as much phosphoric acid and sodium oxide, and half again as much calcium oxide, magnesium oxide, and potassium oxide.

THE PODSOLIZATION AND ITS SILVICULTURAL IMPORTANCE

The data presented show that the amount of organic matter, inorganic colloids (the clay fraction), and chemical elements found in the burnt sienna and yellow horizons is greater than in the leached layer. Likewise, it is evident that these zones are distinctly acid, with the lowest pH in the leached zone, and an upward trend for the soil humus zone and also for the burnt sienna and yellow soils. This factor is of outstanding importance in the explanation of the leaching process. The organic acids are believed to play an important rôle in the removal of the soil salts from the first soil zone and their redeposition in the lower soil layers. In a cool forest floor, an acid condition reduces the activities of fungi and micro-organisms, resulting in incomplete oxidation and decomposition of the organic detritus. These colloidal humic materials, acid in nature, percolate through the first soil zone, where they leach out the bases to form a colloidal suspension. Coming to the second soil zone, the burnt sienna horizon, the presence of more basic materials precipitates these colloidal particles. The dissolved humus substances thus protect the soil colloids from loss, and there is a diminution of bases, especially iron and aluminum, from the leached layer, with their subsequent accretion in the burnt sienna horizon.

As Hesselman ('25) has indicated in his study of humus layers in coniferous forests, silviculture can play a part in the development or retardation of the podsol process. This is true both where the podsol soil is the result of climatic conditions and where it is the result of favoring pure coniferous stands. The controlling factor appears to be very largely soil acidity, since strongly acid conditions in the forest floor are conducive to the leaching process in the soil layers. Slow decomposition and strongly acid conditions go hand in hand. Any silvicultural method which will increase the rate of decomposition of the detritus materials will help to combat the tendency

toward the formation of a degenerated soil. Since a higher temperature accelerates the action of the micro-organisms, thinnings and small openings in the stand will hasten oxidization and decomposition by permitting more solar radiation to fall upon the forest floor. Furthermore, the admixture of hardwoods in coniferous forests should be favored, because hardwood leaves produce alkaline buffer substances which react upon the humic acids. The species most valuable for this purpose are ash, birch, maple, and beech. Not only is the soil directly favored by such a mixture of hardwood leaves in the detritus materials, but the nitrogen transformation is much livelier. This last factor is of decided importance in producing higher yields. While it is true that in this country forestry has not yet reached a stage where the liming of the soil is feasible, as is being done in the beech forests of Denmark, nevertheless we have within our means recognized silvicultural measures which can be utilized to increase soil fertility.

Pure white pine stands in New England tend to produce podsol soil. Fisher ('28) has described this development at the Harvard Forest and its subsequent conversion to a good mull soil. This has been done simply by permitting the better hardwoods to come up in young pine stands. In this region a decided decrease in the rate of growth of pure pine stands takes place at an age of between 50 and 60 years. Not only is there a period of stagnation, but also low quality timber is produced because of the slow pruning. Perhaps such poor growth conditions could be postponed to a much later date by the use of judicious thinnings. Accompanying such a period of stagnation, strongly leached layers with raw humus zones several inches in thickness are developed. When such pure pine areas are clear cut and the subsequent stands permitted to develop into mixed stands composed of scattered pines and the better hardwoods, excellent mull soils are formed where degenerated soils once existed. This change is exceedingly rapid. At Petersham, no trace of leached soil could be found in from twelve to fifteen years after the softwood stands had been cut.

The entire question of podsol soil formation where it does not occur naturally as the result of environmental conditions offers a striking proof of the old German forestry axiom, "Beech to ten per cent of the stem count should be maintained to produce good soil conditions and consequently good growth." Although our beech appears to be much less valuable than the European beech as a soil improver, there are a number of other species which can be made to serve the purpose.

SUMMARY

1. In regions of humid climate, where rainfall is abundant, and winters severe, there exists a tendency toward the podsolization of forest soils. Such soil can also be formed in regions with more favorable climatic conditions as the result of producing pure stands, especially conifers. This soil formation

is characterized by a leached layer, gray in color, immediately beneath the organic horizon; and an enriched horizon, burnt sienna in color, below the zone of outwashing.

2. A physical and chemical examination of a typical northern podsol profile shows that more organic matter, clay particles, and chemical elements are present in the enriched zone than in the leached zone.

3. These conditions are reflected in the maximum water-holding capacity and calculated wilting point determinations made with samples from the various horizons.

4. Cool temperatures and acid conditions further the podsolization process because of incomplete oxidation and decomposition. It is believed that the acid humus particles in the form of colloids leach out the basic materials as they pass through the leached layer, to redeposit them in the enriched zone.

5. A tendency toward podsolization can be combatted by opening up the stand and by encouraging the admixture of hardwoods such as ash, birch, maple, and beech. Such silvicultural measures hasten the activities of micro-organisms and decomposition, produce alkaline buffer substances which react against the unfavorable humic acids, and produce a more lively nitrogen transformation.

To Dr. P. R. Gast of the Harvard Forest the writer wishes to express his thanks for reviewing the manuscript and for his many helpful suggestions.

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LITTORAL VEGETATION ON A HEADLAND OF MT. DESERT ISLAND, MAINE. I. SUBMERSIBLE OR STRICTLY LITTORAL VEGETATION¹

DUNCAN S. JOHNSON AND ALEXANDER F. SKUTCH

Purpose

In the present investigation we have undertaken to determine the precise limits of distribution, vertically and horizontally, of each littoral plant and plant association found on a high, rocky point of Mt. Desert Island, Maine, known as Otter Cliffs. Our object was the discovery of the external conditions limiting this distribution.

Most of the observations to be recorded were made during July, August and early September of the years 1923 to 1925. In March 1927 the junior author spent three days studying the late winter flora of our area, and the senior author followed the seasonal development of the vegetation from June to September of the exceptionally cool and backward summer of 1927.

Area and Methods

Otter Cliffs are on the south side of the island, close by the Ogden Station of the Mt. Desert Island Biological Laboratory, and are completely exposed to the heavy surf of the open Atlantic. They lie near 44° 19' N. latitude and 68° 11' W. longitude. Our work was carried on from the Weir Mitchell Station of this laboratory as a base. The area most carefully studied extends 150 feet north and south, and 300 feet east and west, and includes elevations from -8 to +50 feet (Chart I). It was selected because of the widely varied habitats provided by the rock surfaces of many different slopes and exposures, and by tide-pools of very different sizes at many different levels. It embraces some bottom at 4 to 8 feet below mean low water, of rocky or gravelly character, and a bit of coarse shingle and boulders between 7 and 13 feet above low water, while the rest of the littoral zone is of granite or schist cliffs and ledges, with some trap dikes. Not until the 20-foot level, 10 feet above mean high tide, is reached do we find even minute pockets of soil in

¹ Botanical Contribution No. 87 from the Johns Hopkins University. The authors gratefully acknowledge here the courtesy of the Trustees and of Director Ulric Dahlgren of the Mt. Desert Island Biological Laboratory in affording them the facilities of the Laboratory for carrying on this work. They also here express their thanks to Superintendent George B. Dorr of Lafayette National Park, for help in fastening our tide-stake to the ledges, and for transportation to the area in March 1927. They are indebted also to Doctor A. S. Hitchcock for naming the grasses and to Doctors M. A. Howe, Albert Mann, and W. R. Taylor and J. E. Tilden for identifying various algae collected in the area studied.

crevices of these ledges, where rooting plants can take hold, and only at the 30-foot level does a soil become continuous over considerable areas. There are thus, in the lower parts of our area, no pockets with mud bottoms that might bear *Zostera* (eel grass), a plant which actually withstands a very

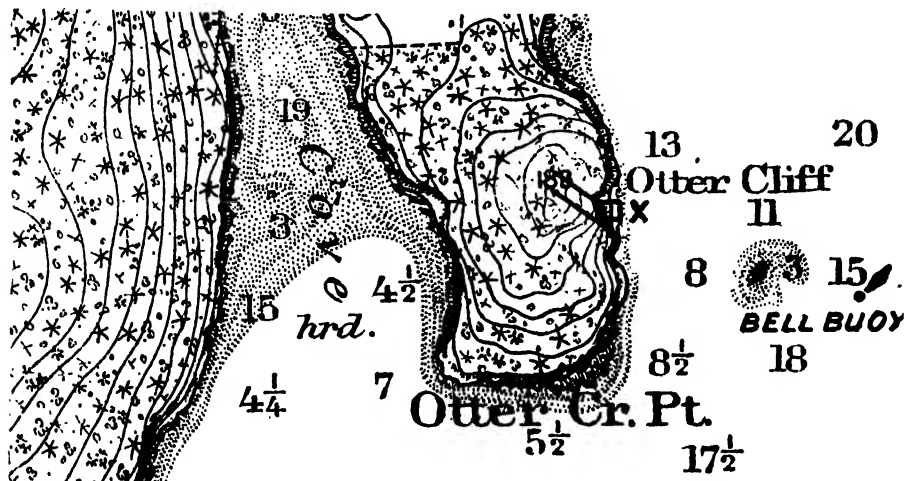


CHART I. The Otter Cliffs portion of the U. S. Coast and Geodetic Survey Chart No. 306, showing, at X, the location of the area studied. Otter Cove is at the left and the small, offshore reef at the right. Scale 1: 36,000.

heavy surf on adjoining shores which are muddy. Our shore is occupied by a series of varied plant associations, ranging from tangles of large kelps or crusts of corallines near low water mark to a dense spruce-balsam forest on the top of the cliffs. Each of the numerous tide-pools is occupied by a series of algae whose kinds and vegetative characters depend on its elevation, exposure and illumination.

The mean range of tide at Otter Cliffs is 10.4 feet, this being the mean derived from the ranges given for the two nearest datum points, by the Tide Tables (1924) of the United States Department of Commerce. Bar Harbor, 5 miles north of Otter Cliffs, has a mean range of 10.5 feet, and Southwest Harbor, 7 miles to the south, has one of 10.3 feet. Our zero datum level, as in the Tide Tables, is mean low water. The accurate determination of the mean low water level at Otter Cliff was finally accomplished after overcoming rather serious difficulties in anchoring our tide-staff to the smooth ledges. We finally secured the staff to timbers wedged in crevices in the ledges and braced it from 1-inch steel dowels cemented in the rock (see Pl. VIII, Fig. 1). After recording the water level at turn-of-tide (usually at low water) on a number of days with all ranges of tide, we compared these figures with the expected readings, obtained by multiplying the predicted level, at turn-of-tide at Eastport by the fixed ratio given by the Tide Tables for Mt. Desert points

in relation to this, the nearest, "reference port." Our zero, so determined, brings the actual and the expected values into close agreement.

The duration of submergence and exposure at any particular level can be read from carefully recorded tide-curves, covering a twenty-five hour period, after the method employed by Johnson and York ('15, pp. 12-14, 131-136), to which reference should be made for fuller details.

Next, we established a base-mark on the highest point of the outer ledge, at 18.8 feet above M. L. W. (Pls. VIII, XII, Figs. 1, 2, 16). By levelling from this with the aid of a spirit level and a long staff, the elevation of each tide-pool and of each important topographic point up to the 50-foot level was

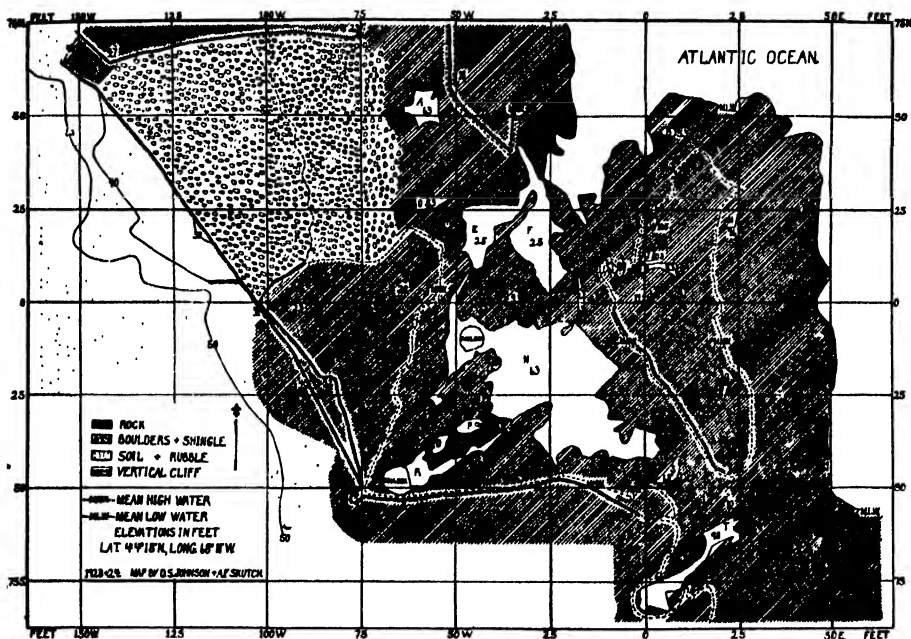


CHART II. Map of the area studied intensively, from mean low water to the 50-foot level. It shows the ledges, boulders, shingle beach and tide pools (levels indicated in feet) as they show at low tide. It also shows the mean high water line and the vertical cliff forming most of the inshore border of the littoral portion of our area. Compare with Figs. 1 and 2, Plate VIII.

determined, and marked by paint on the rocks. Through this base-mark as a center we laid out two axes at right angles, and then series of other lines parallel to each of these axes at intervals of 25 feet. The extremities and some intermediate points on these lines were marked on the rocks. By aid of these, a map was made of the area studied, showing the chief contour lines as well as the tide-pools and the few large detached boulders (Chart II). These same lines on the rock enabled us to determine the vertical and horizon-

tal distribution, over the ledges and through the tide-pools, of the plants on this shore.

We shall find as we proceed that, while each littoral plant is confined to definite, usually narrow, vertical limits, yet the zones or belts of vegetation are less evident to the eye than they are on the gravel, sand or mud bottoms of quieter shores. One reason for this indefiniteness is that each small drainage furrow, transverse to the general shore line, has secondary vegetational belts of its own running transversely to the shore line. The algae of mid-channel in each rill are those characteristic of lower levels (where exposed), while those at each margin of the rill are algae that can withstand more desiccation. Each tide-pool also interrupts the horizontal belt in which it occurs, with its series of different algae which can thrive under constant submergence.

A striking feature of the littoral vegetation belt here, as compared with that on quieter shores, is its elevation to 2 feet or more above the actual average level of the intertidal zone. This elevation is evidently due to wave action. The precise amount of elevation at any point is determined by the effects which exposure and the conformation of the rocks produce on the height of the wave splash.

The two primary habitat zones distinguished on this shore are the true littoral, or submersible zone, extending from 6 feet below to 14 feet above mean low water, and the adlittoral, or terrestrial zone proper, from 14 to 193 feet. The lower edge of the adlittoral zone (14 to 35 ft.) is rarely wetted by wave splash (in the growing season at least), but is commonly wet solely by wind-blown spray. The whole upper portion (35 to 193 ft.) forms a non-halophytic or inland zone which is wetted only by the fine spray that may be carried far by occasional high winds. The littoral zone is occupied by three distinct belts of vegetation, and the adlittoral zone by four distinguishable belts.

The Vegetational Belts of the Submersible Zone are: 1. The Sublittoral Belt, the lowest of the series, which extends from 6 feet below low water to 2 feet above this level. It is characterized by associations of *Alaria*,² *Halosaccion* and *Melobesia*. 2. The Lower Littoral Belt embraces levels from 2 to 7 feet, and is characterized by associations of *Porphyra*, of *Fucus furcatus*, of *Spongomorpha arcta* and *S. spinescens*, of *Ascophyllum* and of *Rhodymenia*. 3. The Upper Littoral Belt extends from 7 to 14 feet, and is characterized throughout the year by associations of *Fucus vesiculosus*, of *Ascophyllum* and *Polysiphonia*, of *Calothrix* and of *Verrucaria*. In summer large patches of *Codiolum* appear on exposed ledges, while in winter and spring *Bangia*, *Ulothrix flacca*, *Entromorpha minima* and *Hormiscia penicilliformis* largely replace the *Codiolum*. It may be remarked here that the

² In case only one species of a genus is mentioned in this work, the generic name alone is usually given. The specific name with the authority will be listed in a subsequent paper (Ecology, Vol. IX, No. 3).

floras of the tide-pools, a discussion of which will be published in a later paper, are necessarily left out of consideration in the delimitation and the discussion of the three submersible belts, and the character plants referred to here are thus those of the exposed rocks and of the shallow trickles.

It will be evident from this outline of the belts of vegetation thus characterized that the splash and spray zones do not here reach nearly so far above high tide mark as do those of the Faeroe Islands, described by Børgesen ('08, p. 708), though in a storm of August 1927 waves, at one point, splashed up beyond 40 feet.

The foregoing remarks, many of which are in the nature of conclusions and might have been reserved for a later section of this paper, are briefly presented this early in order to reveal some of the considerations on which the vertical limits of the belts of vegetation were fixed, as indicated in the succeeding paragraphs, and to suggest some of the facts it was in many cases necessary to learn before we could recognize clear zonal limits, or even to recognize any definite zonation at all.

Sublittoral or *Alaria*-*Halosaccion*-*Melobesia* Belt

(From — 6 to + 2 feet)

The lower limit of this belt is difficult to determine because of the constant agitation of the water. That given above is the limit of the bottom on which we could see, and feel with a long handled hook, that *Alaria* and sometimes *Saccorhiza* were attached. The upper half of this belt was studied with care during low water of spring tides, when, with the receding of the waves to 3 or 4 feet below M. L. W. (mean low water) it was possible to distinguish all larger plants growing down to these levels. The three dominant plants mentioned seem all to be perennial. At least all are common in both March and midsummer.

Alaria esculenta is the dominant plant in this belt and grows abundantly throughout both its horizontal and its vertical extent. (Pls. IX–XI, Figs. 7, 8, 12.) On one rock surface of 1 square foot, situated just above the M. L. W. level, 88 individuals, all over 10 cm. long, were attached. On another square foot nearby 74 plants of this alga were growing, all over 10 cm. long, 37 of them between 1 and 2 meters in length, and two over 2 m. long. *Alaria* may here grow to 2 or even 3.5 m. in length, and have a maximum width of 15 to 18 cm. The lower plants of *Alaria* are in general larger, while those near and above M. L. W. are decidedly smaller in size, many, at its upper limit, having a blade but 3 or 4 cm. in width and 6 or 8 cm. long.

The larger, older *Alaria* plants, pounded by the waves, become much frayed at the tip (Pl. XI, Fig. 12). The thin margins of the blade split transversely—recalling the well-known behavior of the mature leaf of the banana when frayed by the wind—while the tip of the rib is worn off to a

pointed or wedge-shaped end. It seems clear that it is this fraying of the blade that often enables this alga to withstand the impact and pull of the tons of water that are constantly tumbling on it and tugging at its holdfasts. One has but to watch the surge of the waves dashing on it at low water, and see the blades writhe as they are thus lashed about, to realize how tremendous is the mechanical strain to which these large plants are subjected almost unceasingly throughout life. Tests were made to determine the actual strain necessary to break the stipes of the three kelps found in our area. The results of these tests are given in Table I. They show that the stipe of *Alaria* will support a pull of over 45 kilograms per square centimeter of cross section. This is remarkable when the large moisture content of the stipe is considered. They shrink in drying to a small fraction of the thickness they have while living.

TABLE I. *Breaking Strain of the Fresh Stipes of Kelps*

Plant	Weight causing rupture	Cross-sectional area at point of rupture	Weight per square cm.	Mean
<i>Alaria esculenta</i>	$\left\{ \begin{array}{l} 9730 \text{ g.} \\ 8375 \\ 8045 \end{array} \right.$	$\left\{ \begin{array}{l} 0.258 \text{ cm.}^2 \\ 0.197 \\ 0.141 \end{array} \right.$	$\left\{ \begin{array}{l} 37,700 \text{ g.} \\ 42,300 \\ 56,900 \end{array} \right.$	45,600 g.
<i>Saccorhiza dermatodea</i>	$\left\{ \begin{array}{l} 8785 \\ 3800 \\ 3725 \\ 3090 \end{array} \right.$	$\left\{ \begin{array}{l} 0.353 \\ 0.152 \\ 0.132 \\ 0.086 \end{array} \right.$	$\left\{ \begin{array}{l} 24,900 \\ 25,000 \\ 28,200 \\ 35,800 \end{array} \right.$	28,500
<i>Laminaria digitata</i>	$\left\{ \begin{array}{l} 10,905 \\ 15,770 \\ 13,790 \end{array} \right.$	$\left\{ \begin{array}{l} 0.306 \\ 0.335 \\ 0.251 \end{array} \right.$	$\left\{ \begin{array}{l} 35,600 \\ 47,100 \\ 55,000 \end{array} \right.$	45,900

Such observations on the habit of these kelps also make it clear that it is the intercalary growing zone and the basal location of the small, fertile pinnae characteristic of this genus (Pl. XI, Fig. 12 A1), that enable it to thrive where other large Laminariaceae, with reproductive organs located on the more vulnerable, terminal blade, rarely endure long enough to accomplish reproduction.

Even the mechanical features mentioned above do not prevent the *Alaria* from being sometimes torn loose by the relatively moderate summer storms. One even then sees scores of blades broken loose from the stipe, and every now and then a tangle of several blades that seem to have been torn free by the successive rupture of all of the holdfasts or stipes, as the waves threw the strain of the whole tangle of blades now on one stipe and then on another. It is evident that the more delicate, frayed blades of the *Alaria* can become tangled far more readily than the blades of the firm *Saccorhiza* do; and in this respect at least the former are at a slight disadvantage. In March and even in June, 1927, as nearly as could be determined in the tumultuous surf then

prevailing, few large, intact plants of *Alaria* were attached above the level of mean low water. Extending a foot or two vertically above this level was a zone of rock, which could be followed all along the shore, over which were attached numerous "defoliated" holdfasts each supporting at most a short length of stipe, from which the blade had been broken or torn away by the violence of the winter storms. These dismantled holdfasts were, of course, the remains of the uppermost plants observed during the preceding summer.

Saccorhiza dermatodea is the only other large alga that has ever been at all frequent in the sublittoral belt. This species grows to two meters in length and attains a width of ten centimeters. On the rocks directly exposed to the waves this alga in 1923 was outnumbered by *Alaria*, often 100 to 1.

In spots more protected from waves and sun, as in the little notch behind the projecting barrier of rock around 30 N. \times 15 E., *Saccorhiza* may in some years be considerably more abundant and also more luxuriant. The vertical range of *Saccorhiza* is evidently decidedly less than that of *Alaria*, usually extending from -1 foot to $+1$ foot. In rather more protected tide-pools, where the alga is more abundant, small plants of it may sometimes be found even as high as 9 or 10 feet. In September 1926 and June 1927 *Saccorhiza* was not seen either in the sublittoral belt or in the tide-pools.

Laminaria digitata is infrequent on the exposed ledges, but occurs sporadically on the protected, shoreward side and is most frequent of all (in dozens or scores) in the lower tide-pools. In fact, one seldom sees elsewhere two individuals that are near enough together to touch each other. On the shoreward side of the rocks we find in some seasons 4 or 5 plants for each 10 meters of shore-line. The greatest size attained in protected areas by *L. digitata*, as far as observed in 1923, is 1.5 m. in total length and 0.5 m. in width of blade. The plants of the wave zone on the exposed side of the rocks are hardly half this size.

Halosaccion ramentaceum: This coarse, filamentous red alga is by far the most abundant plant at the upper margin of the sublittoral belt. In fact, on sloping rocks, as contrasted with vertical ones, *Halosaccion* is so abundant on the seaward side between $- .5$ feet and $+ 1.5$ or even 2 feet as often to dominate these levels and form a distinct association by itself (Pls. X, XI, Figs. 8, 9, 12). The branched, often rather bushy plants of *Halosaccion* reach a length of about 10 to 15 cm. in early summer, and form dense, close-set stands. It is interesting to find this alga occupying practically the same narrow tidal zone, just above M. L. W., which was dominated by *Chondrus crispus* on the somewhat quieter shores at South Harpswell, in Casco Bay, as was observed by the senior author in 1912-1918. *Halosaccion* persists throughout the year, and plants 12 and 15 cm. long were abundant at Otter Cliffs in March and June, 1927.

Chondrus crispus: Here at Otter Cliffs *Chondrus* has been almost absent from the open, seaward side of the rocks near low water mark, though it does

occur somewhat frequently in tide-pools and on more protected rocks at higher levels. In June 1927, though it was practically absent from our area, *Chondrus* covered many yards of adjoining ledges for a foot above M. L. W. It is hoped that further study of this and neighboring areas may suggest an explanation of the absence of *Chondrus* from the zone which it constantly occupies on the rocky shores of Long Island and of Casco Bay and on certain shores near Otter Cliffs. It at first seemed possible that the absence of *Chondrus* at Otter Cliffs in July and August of 1923 was a chance seasonal vagary and that another summer might see *Halosaccion* replaced by *Chondrus*. But a study of the distribution of these two algae in four later summers showed that *Chondrus* was always relatively sparse, though in September 1926, it was perhaps as abundant as *Halosaccion*. At this season, however, the latter alga was very sparse and short as compared with all previous summers.

Melobesia Lenormandi: This is, after the kelps, perhaps the most characteristic plant in the midlevels of the sublittoral zone. It is a beautiful, pink, encrusting form, found in large patches on the exposed rocks from M. L. W. downward to at least 5 feet below. It is seen also in drainage sluices from the lower tide-pools, as well as in the tide-pools themselves. In all locations where it was found, *Melobesia* is almost or quite constantly covered by water. It seems intolerant of the loss of any of the water contained in its tissues. This coralline is perennial in habit, being quite as abundant in March 1927 as in midsummer.

Ulva lactuca: This is the only green alga that seems really characteristic of the sublittoral belt on the seaward side. It occurs sparingly from M. L. W. up to 2 or 3 feet. It is found sparingly also, in both spring and summer, in sluices from tide-pools, and often abundantly, as will be noted later, in the tide-pools themselves. It is not present where it could be uncovered for many minutes together. The sheets seen are all comparatively small, the larger only a decimeter or so across. There are thus no sheets that can be compared in size with those 10 meters broad that were found on the mud-bottomed, sewage-tainted inner harbor at Cold Spring Harbor.

Petalonia fascia is an unbranched, narrow, ribbon-like, slightly ruffled, perennial brown alga which occurs rather generally along the upper margin of the sublittoral belt, especially in wetter or more shaded places. The plants reach a width of 10-13 mm. and may grow to a decimeter in length. They often form a dense colony of dozens of plants which may cover a square decimeter or more as *e.g.* in the rill shown in figure 7, plate II. It is especially abundant in spring and early summer. The lowest plants of this alga are found at or below M. L. W. but it reaches to the upper edge of this belt and, along the rills, well up into the lower littoral.

Callithamnion floccosum, bearing tetraspores, was found in March 1927

in a small pool near the upper margin of this zone. It has not been recorded during the summer.

Three other macroscopic algæ scattered in this sublittoral belt are forms which are more characteristic of the lower littoral belt, smaller or larger numbers of which wander down into the upper part of this sublittoral region. *Rhodomenia palmata* is the largest and most striking of these inwanderers from the next higher zone which push down toward, or even to, the M. L. W. level. It grows not merely on the rocks, but occurs also as an epiphyte on the stipes of *Alaria*. *Spongomorpha spinescens* is a green alga from the next zone above (Pl. X, Fig. 10) which sometimes settles, sparingly, on the rocks between the bases of the kelps of this sublittoral belt. *Chordaria flagelliformis* occurs, though rarely, associated with tufts of *Halosaccion* near the upper margin of this belt.

These three algæ, once they have found standing ground, seem to grow as luxuriantly here as they do anywhere. It seems clear that they are really kept from becoming more abundant at these levels merely because the kelps and *Halosaccion* have preempted most of the available attaching surface in the upper portion of the sublittoral zone, which is perhaps the only portion of it that affords these small algæ adequate light. Many plants of these algæ that do start on a bit of bare rock here are soon torn off by the tangles of kelps beside them.

Lower Littoral or Porphyra-Fucus Furcatus-Spongomorpha Belt

(From 2 to 7 feet)

The belt so limited is dominated by a distinct set of plants which are found here only (at least in any abundance), though there are also plants of several other species that wander up from below or spread downward from the next belt above. The characteristic plants which distinguish this belt are, in the order of their prominence: *Porphyra umbilicalis*, *Fucus furcatus*, *Spongomorpha spinescens*, *S. hystrix*, *S. arcta*, *Rhodomenia palmata*, *Ascophyllum nodosum*, *Rhizoclonium tortuosum*, *Ralfsia verrucosa*, *Chordaria flagelliformis*, *Elachistea fucicola*, *Ectocarpus littoralis*, *Enteromorpha compressa*, and *Hormiscia Wormskjoldii*. Certain of these algæ may be found as far as a foot or more below this belt, and in particularly wet or shady places some of them may occur a foot, or two, above it. The zone of their general, and really abundant occurrence, however, has the width above indicated.

Of other forms living in this belt, most are species that occur more abundantly just above or just below it. Such algæ are *Chondrus crispus*, *Petalonia fascia* and *Halosaccion ramentaceum*, which creep up from below, and *Fucus vesiculosus*, *Codium longipes*, and *Polysiphonia fastigiata*, which push downward from the zone above.

Porphyra umbilicalis is, on the whole, the most widespread alga of the lower littoral belt. It grows especially abundantly on sharply sloping rocks, often on those thickly covered with barnacles (Pls. X, XII, Figs. 9, 10, 17). Most commonly it is attached to the rock itself, but occasionally to barnacles, and it may also, though rarely, grow as an epiphyte, *e.g.*, on *Polysiphonia fastigiata*, which is itself an epiphyte on *Ascophyllum*. The exposed plants of *Porphyra* may here attain 10 or 15 cm. in length, barely half the size it may reach in more protected areas nearby, *e.g.* at Northeast Branch on Mt. Desert Island and at Sullivan's Falls just across Frenchman's Bay. The constantly submerged plants of the lower tide-pools of our area are decidedly larger than those of the exposed ledges. In some places, between the two-foot and the six-foot levels, there may, in midsummer, be as many as five or even ten plants of *Porphyra* to the square decimeter of rock, and the fronds may completely cover the surface for many square decimeters with several layers of their iridescent sheets. Throughout much of the horizontal extent of this zone, however, *Porphyra* is often far less abundant, with only half a dozen or perhaps a dozen plants to the square meter. During low tide on a bright day, these sheets of *Porphyra* dry down to form quite tough, papery layers, much like thin sheets of dried gelatin, which stick closely to the barnacles or to the surface of the bare rock (Pl. X, Fig. 10). With the first few waves of the returning tide the *Porphyra* again becomes flexible, and the individual sheets are soon freed from each other as they are lashed back and forth by the surf. In March 1927, *Porphyra* was fairly common. In June of 1927, it was extremely abundant, often covering 90 per cent of areas 2 or 3 meters square with plants up to 5 centimeters broad (Pl. XII, Fig. 17). It may be pretty completely ground off the exposed rocks by the floating ice during the winter (See Davis '13), though Kjellman ('78, p. 11) found it abundant in Sweden in winter. The plants shown in figure 17 were almost completely washed off by a summer storm two months later.

Fucus furcatus: This wrack forms the next most important element in the vegetation of the lower littoral belt, and occurs on the wetter, or more shaded areas throughout its whole vertical extent. It is much more abundant, however, in the lower half of the belt, where it may grow in the sun; but it flourishes best on the shaded, inshore side of the outer ledges and beside the narrow channels or furrows through the ledges, which, by confining the waves and causing them to splash higher, subject it to more frequent wetting. In some of these localities *e.g.*, on the ledges just east of our tide-stake, also near 100 S., the long, dichotomous, flat and pointed branches of this *Fucus* cover small patches of the ledge, 30 to 40 decimeters across, as completely as *Porphyra* does elsewhere (Pl. X, Fig. 9). Over most of the belt, however, this *Fucus* is scattered rather sparsely, and wherever the midday sun reaches it for more than an hour during low tide, it shows the dwarfing effect of exposure (*i.e.*, desiccation). Near its upper

limit, *Fucus furcatus* is sterile and is then practically indistinguishable from the sterile plant of *F. vesiculosus* with which it seems to mingle between the 6-foot and 8-foot levels. In March and June 1927, this plant was very abundant in the lower littoral zone and was fruiting profusely. The longer of the linear, flat, receptacles measured 8 or even 10 cm. By July 10, 1927, most of the mature receptacles had turned yellow and begun to soften. In late August few large receptacles were to be seen.

The three interesting species of *Spongomorpha* found on our shore occupy different habitats and also differ in relative abundance from year to year.

Spongomorpha spinescens is usually the most abundant green alga in the lower littoral belt, at least on the seaward side of the ledges. It is less abundant than *Porphyra* on exposed sunny rocks, but it is often very plentiful on shaded rocks and in sluices where the wash from waves flows over it. In such places, the dense tufts, 5 to 8 cm. long and 2 to 3 cm. thick, may stand so close together as to cover half, or even more, of the surface for several square decimeters (Pl. X, Fig. 10). At the lower edge of the belt this *Spongomorpha* sometimes pushes down between the *Alarias*. At the upper edge, it may form dense tangles on steep and shaded rocks. When left above water at low tide the felted tufts of the *Spongomorpha* drain out rather slowly and, as it grows mostly in shaded spots or in little gullies, this alga does not dry out as completely as *Porphyra* does (Pl. XIII, Fig. 21). *S. spinescens* seems an early summer species. Late in August, 1925, it was noticed that areas of the rock which it had occupied were becoming bare. Specimens still attached were decaying, and a very slight pull was sufficient to dislodge them. In March, 1927, this species could not be found on Otter Cliffs. In June, 1927 tufts of it, 6 to 10 cm. long, were common between the 1- and 4-foot levels on most of our outer ledges and up to 7 feet or more in wet or shaded spots.

Spongomorpha hystrix is another species of this genus occurring in this belt where, however, it is almost confined to tide-pools and rills from them. Only when a pool is drained to its lowest level is this *Spongomorpha*, at the edge of the pool, somewhat exposed to the air. Its interesting peculiarities will be mentioned in a later paper dealing with the denizens of the tide-pools.

Spongomorpha arcta is a third species of this genus which, in some seasons at least, becomes very abundant in the lower half of this lower littoral belt. In June, 1927 the bosses of the outer ledge between the 2-foot and 5-foot levels, often over several square meters, were thickly sprinkled with the short round-topped tufts of *S. arcta* (Pl. X, Figs, 8, 9). The tips of many tufts had turned to such a brown color that the plants were at first mistaken for *Bangia fusco-purpurea*. Microscopic examination showed that the contents of the upper 15 or 20 cells of each branch had shrunk away from the walls and turned brown. Cells of the lower, protected parts of

the branches were still green and otherwise normal in appearance. These same tufts persisted in this condition and in considerable numbers till mid-July, after which they gradually disappeared.

Rhodymenia palmata is, after, *Porphyra*, the most important member of the Florideae found in this belt. It is, however, not characteristic of the whole width of the Lower Littoral as *Porphyra* is, but is usually confined to the lower half of it. Here it may cover the substratum over small, shaded, areas, but it is never as generally abundant as *Porphyra* or even as *Fucus furcatus*. Like this *Fucus*, *Rhodymenia*, except where very near low water level or to tide-pools is confined to shaded and wave-splashed steep ledges (Pl. XI, Fig. 12). Many plants of the *Alaria* gathered from M. L. W., or lower, bore numbers of vigorous fronds of *Rhodymenia* as epiphytes, showing that when well lighted, as here, where they float up near the surface at low tide, supported by the *Alaria*, this red alga can grow in the sublittoral belt. On the other hand, where exposed to wash by exceptionally high waves, as on a ledge at 90 N \times 30 W and also on the rocks beside a shaded gulch in the ocean shore, half a mile north of our area, the *Rhodymenia* was able to push up to as high as 7 feet above M. L. W. The plants of *Rhodymenia* seen in March 1927 were chiefly battered bases which bore numerous young proliferations, some of them 6 cm. long. In June plants of 15 cm. length were common.

It is interesting also to note that at Sullivan's Falls, 15 miles from our area, on a sunny, quiet shore, *Rhodymenia* gets up to but 1 foot or rarely to 1.5 feet above M. L. W. and goes downward but a foot or so below this. The narrow vertical range of this alga at Sullivan's Falls is probably to be attributed to the fact that, on this smaller body of water, the wave action is very slight as compared with the open shore of the Atlantic at Otter Cliffs.

Ascophyllum nodosum: This perennial coarse wrack is almost as prominent in the upper third of the belt we are discussing as *Fucus furcatus* itself. On the exposed seaward side of the ledges, *Ascophyllum* is represented in summer by relatively few worn stumps of stalks a decimeter or two in height, with small regenerated flat branchlets. In more sheltered areas, e.g., about Tide-Pools A, B and N, the *Ascophyllum* grows to long, tangled fronds with many branchlets (Pl. XII, Figs. 15, 16.) The single fronds may become 5-6 dm. long when growing on rather gently sloping ledges or on the boulder beach. It rarely occurs over any large area in a pure stand. *Ascophyllum* seldom grows near low water mark and, though it often floats on the surface of the tide-pools of this belt (Pl. XII, Figs. 15, 16), it rarely persists where constantly submerged. Only two or three submerged plants of *Ascophyllum* could be seen when carefully looked for in 1926. These were rather spindling and were attached at a depth of about 1 foot in Pool N. The zone of greatest frequency of *Ascophyllum* lies between that of *Fucus furcatus*, with which it mingles in its lower reaches, and *F. vesiculosus*, among

which it occurs higher up, as we shall see. In March and June 1927, the *Ascophyllum* bore scores of ripe fertile clubs on a single plant (Pl. XII, Fig. 15). In midsummer very few of these are seen, and in August, 1927, all mature clubs had dropped off.

Rhizoclonium tortuosum: Though this striking green alga is absent from the exposed, well-drained rocks throughout this belt, its felted tangles do occur, somewhat above, as well as below the water surface of pools and rills (Pl. XIV, Fig. 24). It is therefore merely mentioned here, but will be described more fully in a later paper dealing with the tide-pools.

Ralfsia verrucosa: This encrusting brown alga, although not conspicuous, is very frequent in the lower littoral belt, where it may grow on well-drained rocks, and has a wide vertical distribution, being found in pools even above mean high water level (March 1927). It is restricted to shallow water at the edges of tide-pools, and to trickles over the rocks. In such places it forms velvety, sometimes warty, brown, irregular patches on smooth rock surfaces, sometimes several centimeters across.

Chordaria flagelliformis: This coarsely filamentous brown alga is found in the lower littoral belt more abundantly than anywhere else, though it may, on the exposed seaward side of a ledge, go down into the upper portion of the sublittoral belt, where it is, as noted above, frequent among the tufts of *Halosaccion*. In the lower littoral belt it is found almost exclusively either in or close beside tide-pools, or in little gullies, chiefly in the lower half of the belt. Most frequently the much-branched individuals of *Chordaria*, 2-3 dm. long, occur singly, and these are always attached directly to the rock. This is apparently also a summer species with us, and a careful search in March, 1927, failed to reveal its presence. Young plants, 6 or 8 centimeters high, were common by June 15, 1927. Plants up to 5 centimeters were growing on boulders that had been sterile when placed in Pool N on March 30 preceding.

Elachistea fucicola: The distribution of this small, epiphytic brown alga in our area follows closely that of its host, *Fucus furcatus*, which the *Elachistea* infests quite generally throughout its range. It was not found on *F. vesiculosus*. In general, *Elachistea* is most abundant near the upper margin of the range of its host. Copious tufts of it were present in June, 1927. The extreme range noted for *Elachistea* is from the 4-foot level (at 10 N. by 40 E., and 40 N. by 20 W.) up to 7.5 feet (at 40 N. by 30 E.).

Ectocarpus littoralis: This small, delicate brown alga occurs sparsely on the flatter and wetter ledges from mean low water up to 4 or 5 feet. On the whole it is rather more frequent in this belt than in the sublittoral belt, though never conspicuous in either.

Ectocarpus sp. an epiphyte on *Fucus vesiculosus* near Pool A, was found fruiting in March 1927. It may be found elsewhere in winter.

Enteromorpha compressa: This green alga occurs most abundantly, in

summer at least, in the upper half of the lower littoral belt, though it is also found in the lower half of the upper littoral. The lowest plants seen were at about the 3-foot level, the highest at 10 feet. It is more abundant on the shoreward side of the ledges, where it is usually restricted to well lighted, but not too well drained, areas. This is a moderately coarse *Enteromorpha* which grows in dense tufts, often of dozens of plants per square decimeter. The individual filaments often reach a length of a decimeter and have a diameter ranging from 2 to 4 mm.

Hormiscia Wormskjoldii: This is another green alga, which though not found at all in summer, did dominate over a restricted area near the 3-foot level, near 25 N. \times 15 W. in March, 1927.

Turning now to the half dozen algæ which though more abundant in either the sublittoral belt or the upper littoral, may nevertheless occur more or less frequently in the lower littoral, we will consider first the invaders from below.

Chondrus crispus is, as we have seen, relatively sparse in the sublittoral belt. A few patches of it, however, do get above the lower edge of the lower littoral, outside the tide-pools, in which it is generally present. For example, in a shaded crevice at 40 N. \times 20 W. *Chondrus* grew at the 7.5-foot level. At 30 S. \times 8 W., where protected by mats of *Fucus* and *Ascophyllum*, diminutive plants of *Chondrus* reach the 9-foot level. In exposed situations, however, it rarely gets more than 3 or 4 feet above M. L. W.

Petalonia fascia: The narrow, ribbon-like fronds of this brown alga are more characteristic of the upper 2 or 2.5 feet of the sublittoral belt, but are still common in the lower part of the lower littoral. Here, however, it is practically confined to the rills that drain the tide-pools, or to those on the seaward side of the ledges where the water concentrates as the splash from each wave runs downward from the rocks above. In these rivulets the plants may, as in 1923, occur in dozens or scores in a meter's length of the narrow rill (Pl. IX, Fig. 7), *i.e.*, as thickly as they do in the sublittoral belt. The highest plants of *Petalonia* seen were those in Pool T at 10 feet and Pool G at 10.5 feet. In early September 1926, no *Petalonia* could be seen either in the lower littoral or at the edges of tide-pools, where it had been abundant in midsummer in previous years. In June, 1927, ribbons of this alga, 8 to 12 cm. long, were found in tufts of a dozen or more plants attached to *Mytilus* and *Balanus* as well as to the rock, along the rill from Pool T.

Halosaccion ramentaceum: This is another of the Florideæ from the sublittoral belt that creeps up about a foot into this lower littoral. Like the *Petalonia* found in this belt, it is confined to wetter places, *i.e.*, to the little drainage gullies and to the edges of tide-pools.

Four algæ characteristic of the upper littoral belt often overlap into the lower littoral.

Fucus vesiculosus: the most widely spread and conspicuous alga of the next higher belt, may become very common locally in the upper quarter of the lower littoral. Between the 5-foot and 8-foot levels, this *Fucus* is mingled abundantly with *F. furcatus* and *Ascophyllum* (Pls. XII, XIV, Figs. 16, 23) and at higher levels with *F. filiformis*. The sterile plants of the three species of *Fucus* are not easily distinguished in the field, but from the distribution of such individuals as bear fruits, it seems clear that the first two species mingle freely in a zone about 2 feet wide.

Codiolum longipes: In July, 1923, this green alga was widely dominant in the upper littoral belt and was also established on the upper edge of the lower littoral, down to 5.5 feet (Pl. IX, Fig. 5). In later years, it has been less common in the upper littoral, but has remained about equally abundant on the boulders of this lower belt. The habit of this interesting, gregarious seaweed will be more fully discussed when we discuss the next higher belt, where it is most at home.

Polysiphonia fastigata: This is an epiphytic red alga characteristic of the next higher belt, that may be associated with its host *Ascophyllum* where the latter is flourishing in the upper margin of the lower littoral belt (Pl. XII, Fig. 15). The *Polysiphonia* becomes as vigorous at the upper edge of this belt, where found at all, as it does anywhere on the shore.

It will be evident, from what we have said of the lower littoral belt, that it is occupied by a much larger variety of plants than are found in the sublittoral. When we come to discuss the upper littoral, we shall find that it also has a less varied population than the lower littoral. Moreover, while there are several algæ, e.g., *Enteromorpha compressa*, *Spongomorpha spinescens*, *Elachistea*, *Fucus furcatus* and *Porphyra*, that are rather generally distributed across the whole vertical width of the lower littoral, and which thereby definitely characterize it, the greater number of individuals of the other species of this belt are to be found only near either its lower or its upper margin. The chief exceptions to these distributions are to be found among the denizens of the tide-pools which will be discussed together in a separate paper. Hence the denizens of pools in both this belt and the upper littoral belt are referred to only incidentally. Not only is the plant population of the lower littoral belt more diverse in any one season, but it is also more variable from season to season of the year, and at the same season in successive years.

Upper Littoral, or *Fucus Vesiculosus*-*Ascophyllum*-*Calothrix*-*Verrucaria* Belt

(7 to 14 feet)

This belt is characterized throughout the year by an abundance of three perennial algæ and one perennial lichen. Two of these algæ, *Fucus vesiculosus* and *Ascophyllum nodosum*, may be found across nearly the whole width

of the belt, while the third alga, *Calothrix scopulorum*, and the lichen, *Verrucaria striatula*, are confined to the upper two-thirds of it.

Near the lower edge of this belt the perennial epiphytic *Polysiphonia fastigiata* is found accompanying its host *Ascophyllum*, while *Porphyra umbilicalis* is represented here by a sparse scattering of invaders from the lower littoral.

Toward the upper edge of this belt there are blackish green patches of *Calothrix*, some of which are nearly pure, while others show, at the proper season for each, more or less of an admixture of *Bangia*, *Ulothrix* or *Hormiscia*. *Enteromorpha minima* is most frequent in early spring; but may also persist on wetter ledges till midsummer or later. In fresh water trickles near this upper edge of the belt and somewhat above it, *Enteromorpha micrococca* forms curly tangles (apparently perennial) on shaded vertical cliffs.

In summer another set of algæ are found in patches variously interspersed with the perennial species mentioned above. Velvety felts of *Codiolum longipes* and less frequent coatings of *Enteromorpha compressa* may then form almost pure stands over square meters of the rounded bosses of the ledges and boulders which have not already been occupied by the perennial species or by barnacles.

In winter and spring still another set of algæ, all three of which are absent, or inconspicuous in summer, appear in pure or mixed stands on the same bosses which in summer bear *Codiolum* or *Enteromorpha*. These three algæ are: *Bangia fuscopurea*, *Ulothrix flacca* and *Hormiscia penicilliformis*. A fourth species: *Monostroma grevillei* is found scattered sparsely over these levels in spring and early summer.

In addition to these perennial and transient species of algæ that grow exposed on the ledges here, half a dozen other (perennial?) algæ of this belt are confined to the bottoms or edges of the tide-pools or of the rills that drain them. The chief of these are: *Ralfsia verrucosa*, *Gigartina mammilosa*, *Spongomorpha spinescens*, *Rhizoclonium tortuosum* and *Fucus filiformis*. The distribution of these algæ will be discussed in a general description of the denizens of the tide-pools that is to be published later.

The precise distribution of each of the characteristic algæ of this upper littoral belt, outside the tide-pools, is given in the following paragraphs.

Fucus vesiculosus usually dominates on steep, moist or shaded ledges of the upper littoral belt, just as (in summer) *Codiolum* dominates on exposed ones. Its chief competitor in such areas in the lower half of this belt is *Ascophyllum*, of which we shall speak in detail later on. The *Fucus*, like *Codiolum*, is found at all levels across the whole of this belt. It is most abundant and most luxuriant between the 8-foot and the 12-foot levels, where it often dominates considerable stretches of the shore. This species of *Fucus* flourishes about Tide-Pool N where it finds the shaded rocks and large boulders that suit it best. (Pl. XII, Fig. 16). Between 8 and 10 feet

above M. L. W. this *Fucus* grows in dense stands of plants that may, in summer, often reach 2 dm. in length and bear numerous fertile receptacles. Above the 10-foot level, the plants, except in wetter crannies, gradually become smaller, more scattered and nearly or completely sterile.

This *Fucus* bears few epiphytes as compared with the *F. furcatus* which grows lower down. It seems clear that the more rigorous conditions, especially the desiccating power of the air, which restricts the size and the upward spread of the *Fucus* itself, are still more quickly effective on the epiphytic *Elachistea*, and thus prevent it from growing at levels as high as those which its host can endure. The highest plants of this *Fucus* were found at 14 feet, in the shaded recess of the cliff at 52 S. by 75 W., where the atmosphere is kept moist by a fresh water trickle from the rocks.

Ascophyllum nodosum: We mentioned, when speaking of its occupation of the lower littoral belt, that this alga forms its densest growths, attains its greatest size and bears the densest population of epiphytic *Polysiphonia* near the lower edge of the upper littoral belt, i.e., between the 6-foot and the 8.5 or 9-foot levels, as e.g. about Tide-Pool N, where it dominates large areas of the almost horizontal rock surface from 6.5 feet upward. At low tide, the long, monopodially branched fronds of this alga lie on the rocks, or float over the *Spongomorpha* on the bottoms of the pools (Pls. VIII, XII, Figs. 1, 16). Though the gentler slopes are usually more completely covered by *Ascophyllum*, there are also many vertical, shaded rock faces which also bear an abundance of this alga. In the tide-pools, *Ascophyllum* is often present where its fronds float at, or slightly above the surface. This alga is rarely found where it would be submerged at low tide, except in a couple of the most elevated and sunny pools, such as a portion of Pool K at 11.3 feet.

Ascophyllum ranges in size from mere stumps, with short "renewal branches," such as are found on the seaward side of the ledges at levels from 4 to 7 feet, up to abundantly branched fronds 5 or 6 dm. in length. Such large plants occur between the 6-foot and 9-foot levels on the somewhat protected areas about Tide-Pools N, E, F, etc., and on the lower rocks of the boulder beach, west of the tide-stake. It is in these more sheltered areas with gentler slopes, between the 7-foot and 8-foot levels, that the large plants of *Ascophyllum* dominate completely (in some seasons at least) over *Fucus* and *Codiolum*. The latter succeeds the *Ascophyllum* above, often occupying the upper part of the same boulder that bears *Ascophyllum* (or *F. vesiculosus*) a few inches below, as on rock 7 in figure 22, plate XIV. Though abundant each summer this alga has usually borne very few fertile clubs. In March and early June, 1927, however, the mature plants were fruiting heavily (Pl. XII, Fig. 15). By August, 1927 all mature clubs had dropped off. Large tangles of *Ascophyllum* were torn loose by the storm of August 24, 1927, but the dense mats about Tide-Pool N. still persisted.

Calothrix scopulorum is a perennial alga that forms the most abundant

and most constant constituent of thin blackish green crusts, which cover many square meters of the outer ledges between the 9-foot and 12-foot levels (Pl. VIII, Fig. 4). Another frequent constituent of these crusts is a globular, apparently protococcoid alga. These crusts, which sometimes (Fig. 4) almost merge into the nearly jet black crusts of the lichen *Verrucaria*, evidently persist throughout the year, as they are as well developed in spring and early summer as in the autumn (see Kjellman, '78, p. 12).

Verrucaria striatula is a lichen that is very abundant, especially on the shaded rocks of the upper half of this upper littoral belt. On the exposed, sunny sides of ledges it forms scattered dots, or splashes, in the damper pits in the surface of the rocks. On the shady side of a ledge this lichen often forms continuous black coatings over many square decimeters of rock down to, and even in among, the higher *Fucus* and *Balanus* (Pls. VIII, XII, Figs. 3, 16). On the sunny side the lowest crusts of *Verrucaria* lie close to, or mingle with, the uppermost *Codiolum* and even *Bangia*. These black patches of *Verrucaria* persist throughout the year and probably for many years in succession.

This *Verrucaria* is one of the few lichens that can withstand prolonged submergence in salt water.³ When high tide occurs at night they must often stay saturated with salt water for 10 or 12 hours continuously, though actual submergence may last but 2 or 3 hours. With this capacity for withstanding salt water, it seems probable that it is the reduction of the light by overlying water at high tide that fixes the lower limit of distribution of this lichen. This explanation would be quite in accord with the findings of Plitt ('21, p. 61) who shows that lichens in general are distinctly partial to at least moderately well-lighted habitats.

Polysiphonia fastigiata: This blackish species of the Florideæ is the most conspicuous macroscopic epiphyte in the whole of our area. It is often very abundant indeed in the lower third of the littoral belt. It is always epiphytic and is practically always on *Ascophyllum* (Pl. XII, Fig. 15). In a few cases young plants of *Polysiphonia* grew on older ones. It forms dense, dark tufts attached to the main axes and older lateral branches of the *Ascophyllum*, with sometimes half a dozen tufts per running decimeter of such a branch. Each tuft of *Polysiphonia* is 4 to 6 cm. in height and consists of scores of branches in its upper part, though all of these spring from one parent basal filament. The blackish color of the epiphyte distinguishes it sharply from its lighter colored host.

Like its host, this *Polysiphonia* seems to be persistent throughout the year. It was abundant and mature in both March and early June, 1927.

Polysiphonia violacea: Bits of this species were identified among algæ collected at Otter Cliffs in March 1927. It has not been seen in summer.

³ Dr. C. C. Plitt finds 5 intertidal species of *Verrucaria* on the protected, north shore of Mt. Desert Island.

Porphyra umbilicalis: This relative of *Bangia* is so capable of enduring submergence that it occurs abundantly, as we have seen, down to the lower limit of the lower littoral belt at 2 feet. But *Porphyra* is nevertheless so well able to withstand prolonged desiccation that on steeper cliffs, exposed to the full force of the waves, this alga may be found several feet above the upper edge of the lower littoral zone. In particularly favorable places well-developed plants of *Porphyra* may even be found at the 11-foot level. *Porphyra* also occurs occasionally in the tide-pools of this belt.

Enteromorpha micrococca: is a fine perennial species which forms curly tangles on steep rocks wet by dripping fresh water. These tangles occur in the lower edge of the next higher vegetational belt, but at two points in our area they follow these trickles down into this upper littoral. Figure 20, plate XIII, shows a fine tangle of this alga growing 50 yards south of our chosen area.

Codiolum longipes: While *Codiolum* may occur sparsely, as we have seen, in the upper portion of the lower littoral, it is in this upper littoral belt that it grows most abundantly, and in most summers is widely distributed across the whole belt. Here it is most luxuriant on the convex, gently sloping bosses and ledges of the seaward side, and on stable boulders of the shingle beach where fully exposed to both the sun and the waves (Pls. IX, XIV, Figs. 5, 22). In such places *Codiolum* forms, from midsummer on, dense, smoky green, lubricous turfs, which when wet make walking on these rocks extremely treacherous. *Codiolum* is distinctly a summer species. It was not to be found in March 1927, and in June of that year it formed only a very thin coating, a few decimeters square, not covering the rock surface, though quite continuous. The individual plants were 1/3 mature size. These felts may in some places and in some summers, extend pretty continuously from the 6-foot level, up to 11 feet or even higher, and may far exceed *Fucus vesiculosus* in area covered on the exposed ledges. In the summers of 1923 and 1924 *Codiolum* colonies covered many square meters on the seaward side of the outer ledge of our area (Pl. IX, Fig. 5), completely excluding all other megaphytic algæ and forming pure stands. Now and then at lower levels a sheet of *Porphyra* would be found in the midst of such a colony of *Codiolum*, attached either to the rock itself or to the shell of a barnacle. In other summers, as in 1925, 1926, and 1927, the same rock surfaces were largely occupied by barnacles (Pls. IX, XII, Figs. 6, 14) whereas in 1923 these animals had been confined, at the high levels, to the moister furrows between the convex bosses of the rock (Pl. XII, Fig. 13). In March and June of 1927 this part of the ledge was practically bare of *Codiolum*. The major part of the surface was occupied by *Balanus* while the rounded bosses were often completely covered with *Bangia* (Pls. IX, XI, Figs. 6, 11).

Toward the end of August and in early September, 1923, the epiphytic

diatom *Fragilaria striatula* covered extensive areas of the *Codiolum* turfs, as well as the shells of the barnacles growing between them, with a rusty brown coating that gave the *Codiolum* the appearance of being sunburned and dying. Just what harm this smothering brown layer may inflict upon the *Codiolum* is as yet undetermined. It is of interest to note that Mt. Desert Island apparently marks the southernmost point on our Atlantic Coast at which this diatom has been collected.⁴

While *Porphyra* and the diatom just mentioned may thus be very closely associated with the *Codiolum*, it is noteworthy that usually when barnacles occur near this alga, each barnacle or each group of them is separated from the *Codiolum* by a ring of bare rock about a centimeter broad (Pl. XIII, Fig. 18). No explanation of the apparent inability of the alga to occupy the rock next to a barnacle has yet been found, and it is but fair to mention that in the case of old established colonies of the crustacean, the *Codiolum* may grow almost in contact with the animal's shell. It has not, however, been found actually attached to the shell of a barnacle. On a nearby part of the shore, at Seawall, boulders were found in the upper littoral belt with the whole seaward side covered continuously with the *Codiolum*, except for several circular areas about 2 cm. in diameter in the center of each of which was a small depression about 5 mm. in diameter (Pl. XIII, Fig. 19). This depression was always found occupied by a small snail which had evidently kept the ring bare by feeding upon the *Codiolum*. The alimentary tracts of the snails from such depressions were often full of *Codiolum*.

With every low tide on a sunny day the club-shaped filaments of *Codiolum* cling together laterally in little tufts, which separate from neighboring groups to expose the colorless stipes in irregular whitish lines surrounding the areas where the dark green tips adhere. (Pl. XIII, Fig. 18). The appearance of these patches of *Codiolum*, when dried out, is a perfectly characteristic one that recalls the color contrasts or "grain" of so-called Spanish leather.

The lowest patches of *Codiolum* seen were at the 5.5-foot level, the highest at 14 feet. The largest patches of *Codiolum* on the convex surfaces of the seaward side of the ledges are between the 8- and 12-foot levels. It is here that the treacherous velvet carpet is most prominent as one looks over the shore as a whole. Back of the barrier ledges, where the waves break on or splash over great boulders or a gentle slope of the ledge, there may be considerable patches of *Codiolum* at still higher levels, up to 13 or even 14 feet, which resemble the turfs just mentioned but are not as extensive, as completely continuous, nor are they often as dense as those near the 10-foot level (Pl. IX, Fig. 5). The largest boulders of the shingle beach (e.g. near 25-50 N. \times 75 W.) often bear dense felts of *Codiolum* on their

⁴ Communication to the authors from Professor C. S. Boyer, who kindly determined the specimens.

exposed tops, while the smaller, mobile boulders bear no algæ at all. The storm of August 24, 1927 rolled the boulders of the shingle beach about so vigorously as to grind off much of the *Codiolum*, or left the felts of the alga on them turned directly townward and so destined to perish from lack of light. From the distribution of *Codiolum*, it is clear that this alga is one which can withstand pretty prolonged drying, though it is rarely out of reach of the waves of each high tide, or at least of their spray. It is thus practically always washed twice a day, and is of course pretty sure to keep moist during darkness, or even when shaded, by moisture attracted by the salts left in it after the sea water evaporates. The higher patches especially are subjected to prolonged wetting and leaching by fresh water, during the rains which occur while the tide is low.

Codiolum plants attached to a boulder withstood 7 days of drying on a shelf in our laboratory, and others 8 days drying on a ledge above high tide, and when later returned to the beach the plants in both cases continued to live. This experiment shows the ability of *Codiolum* to withstand more prolonged desiccation than it would normally be subjected to anywhere between the extreme tide levels at Otter Cliffs. On the other hand, while *Codiolum* can withstand prolonged drying, and also wetting by fresh water, it is evident from its distribution that it cannot endure submergence in sea water continuously, or even nearly continuously. For no patches of *Codiolum* are found nearer mean low water than 5.5 feet. None occur where submerged in tide-pools nor, as we have seen, does this alga grow in the furrows of the rock, where the water draining from tide-pools would run over it during low tide. Its inability to endure continuous submergence was also proved experimentally. Boulders covered by this alga were left submerged in Tide-Pools N and O, and were found bare of all living plants of *Codiolum* after 15 to 25 days. These relations of the plant to exposure and submergence are similar to those presented by many algæ of both the upper and lower littoral belts. Such algæ, though very different in vegetative structure from the mosses and seed plants of the seashore, evidently have something in common with them physiologically, since, like all the latter on this shore, they cannot endure continued submergence. It is, however, difficult to understand why this *Codiolum*, whose relatives succeed so well where constantly submerged, should never grow thus itself. The only suggestion offering itself is that this habit may be connected with the permeability of the cell walls. But it is hard to see how the diosmotic exchange of substances through such a gelatinous wall as that of *Codiolum* could be less satisfactory when the plant is constantly submerged than when it is alternately dried and wetted.

Enteromorpha minima: After *Codiolum*, this *Enteromorpha* is, in summer, the most characteristic green alga of this belt, outside the tide-pools. It is found (1923 to 1927) chiefly on somewhat shaded, steep faces of

the cliffs, where often splashed by the waves, but out of reach of wave-flow rivulets. At higher levels, 10 feet and upward, it is oftenest found where shaded or moistened more or less by trickles of fresh water. In such places it may completely cover the rock surface for many square decimeters with a bright green turf, which when dry becomes whitish or milky green in color. During low tide of bright, windy days these plants dry out to a crisp, so that they may be rubbed to a powder between the fingers. In spring and early summer an *Enteromorpha* of apparently this same species is common on the seaward slope of the ledges, e.g. near the outlet of Tide-Pool T. This *E. minima* is connected by a seemingly complete series of intermediate forms with typical *E. micrococca*, the distribution of which was noted above.

Enteromorpha compressa: Though this *Enteromorpha* may, in summer, be rather frequent below the zone we are discussing, it is in spring a common constituent of this upper littoral belt. It is here restricted to wetter places at the edges of pools and of small rills, where it forms tufts of simple filaments that stream back and forth with the surging water, as in the drainage furrow shown in figure 7, plate IX. It nowhere grows densely enough to cover considerable areas, but seems rather to fill in small bits of rock surface that chance to be left bare of *Fucus* and barnacles. This alga seems limited to areas where it can never be dried out as completely as *E. minima* may often be, and where it is clear of fresh water. In such situations, it is distributed generally through the lower third of this belt. *E. compressa* is not as abundant at Otter Cliffs as *E. intestinalis* is at similar levels (but always near fresh water rivulets) at Cold Spring Harbor (see Johnson and York, '15, p. 96).

We now turn to the three algæ that are nearly, or quite, lacking from this belt in summer, but which appear, and may become rather prominent in winter and spring.

Bangia fusco-purpurea: This often diminutive red alga, like *Codiolum*, differs markedly in abundance in different summers, but whenever present, is practically confined to this upper littoral belt. It has been found as low as 4.5 feet and as high as the 13.3-foot level, but it is never abundant except between the 8-foot and 12-foot levels.

This alga occurs most abundantly on the rounded, wave-beaten bosses of the outer ledges and on the smooth tops of boulders. Here, on portions of the rock surface not occupied by *Codiolum* or barnacles, *Bangia*, in July 1923, formed very scattered, brownish tufts rarely more than a centimeter or so in height. In other summers these tufts may stand close enough together to form open patches of a decimeter in diameter. The patches have, in midsummer, never been large enough or numerous enough to form a distinct zone on any part of the shore. In more protected areas, behind the outer ledge, *Bangia* is found occasionally, usually much scattered, and here it may grow to longer filaments than where beaten severely by the

waves, as it is on the ocean side of the ledge. In March 1927, continuous patches of *Bangia*, often half a square meter in area, grew on the outer faces of the ledges. These were present in June, 1927, but by July had disappeared as if by weathering off, from the middle outward. By August 15, few clumps larger than one's hand were to be seen. The patches of *Bangia* when dry had a light tan color, while when wet they became a dark chestnut brown. The length of the filaments of *Bangia* in spring was often 6 centimeters or more as compared with the 1 or 2 centimeters in the sparse tufts found in midsummer. One patch 3 or 4 decimeters in diameter persisted till September 6, 1927 (near 100 N. \times 70 W.).

Ulothrix flacca was found in March, 1927 growing abundantly on the smooth seaward face of the outer ledges and on the boulders of the shingle beach, up to the 10-foot level, or even the 12-foot level. It formed, by itself, or often mixed with *Hormiscia*, a thin slimy, green coating over areas half a meter in diameter or more. A few patches of this alga were still to be seen on June 15, 1927, but all had disappeared by August 1. Further observations are needed to show whether it is a regular occupant of these ledges.

Hormiscia penicilliformis is another green alga that was first seen in March, 1927, and which also persisted till early summer. It may grow in relatively pure stands, of filaments 2 or 3 cm. long, on the ledges or boulders, or it may be mixed with *Ulothrix flacca*. Toward its upper limit *Hormiscia* often mingles with *Calothrix* in forming the blackish crusts on exposed rocks, as at the 16-foot level near our bench mark. On the outer face of the ledge *Hormiscia* is most abundant in the lower half of the upper littoral belt.

Monostroma grevillei is another Ulvaceous genus which may occasionally appear in this belt. It then usually occurs toward the lower border of the belt and on the rocks and in rills of the exposed seaward side.

The vegetation of this upper littoral belt is then, as we have now seen, more varied than that of the sublittoral one. In fact, if we include the tide-pool species of these levels, the vegetation is about as varied as that of the lower littoral belt. In midsummer, most of the plant-covered surface, outside the tide-pools, bears *Fucus vesiculosus*, *Ascophyllum*, *Codiolum*, and, near the upper margin of the belt, *Calothrix* and *Verrucaria*. In winter and spring *Bangia*, *Ulothrix* and *Hormiscia* occupy much the same areas that in summer are commonly covered by *Codiolum*. The algae characteristic of this belt are in general those able to withstand a considerable amount of desiccation. There is no alga of the lower littoral belt that shows a resistance equal to that of *Codiolum*, save only *Porphyra*, which may sometimes cover square meters of rock surface in the lower half of this belt, as *Fucus* and *Codiolum* do farther up.

Summary and Conclusions

1. The foregoing is part of a report of an ecological study of the vegetation of a rocky, exposed area on the ocean shore of Mt. Desert Island, Maine. It was made during the summers of 1923 to 1927, and in the last week of March 1927.

2. The area studied extends 150 feet along the shore line, while perpendicular to this it reaches from 6 feet below mean low water upward to the top of the Peak of Otter at 193 feet above mean low water. The portion of this area dealt with here, includes a series of intertidal rounded ledges and of steep cliffs, facing the open Atlantic, among which nestle numerous tide-pools of all sizes and at all levels. It includes also an intertidal strip of shingle beach strewn with rounded pebbles and boulders, from a few inches up to several feet in diameter.

3. One main aim of this study was to determine the exact vertical distribution, with reference to tide levels, of the plants found here. We attempted also to correlate the observed vertical and horizontal distribution with the character of the substratum, and with all those other environmental factors, such as light, temperature, salinity, acidity, and evaporation, which are affected by the alternating submergence and exposure of the plants by the tides.

4. The mean range of tide on our shore is 10.4 feet. After determining the mean low water level, by aid of a tide-staff, we fixed a bench mark on the top of an outer ledge at the 18.8-foot level. The elevations of the various plants and plant habitats were determined by levelling from this bench mark. The horizontal distribution of each plant was determined by aid of a system of coordinates of which the bench mark was the center.

5. In the littoral or submersible region three zones, occupied by characteristic belts of vegetation are recognized: *a.* The sublittoral belt, extending upward to 2 feet above mean low water and characterized by the kelp *Alaria esculenta* and by the red algæ *Halosaccion ramentaceum* and *Melobesia Lenormandi*. *b.* The lower littoral belt, extending from 2 to 7 feet above mean low water and characterized by *Porphyra umbilicalis*, *Fucus furcatus*, and 3 species of *Spongomorpha*. *c.* The upper littoral belt covering levels from 7 to 14 feet, and characterized the year through by *Fucus vesiculosus*, *Ascophyllum*, *Calothrix* and *Verrucaria*. In summer *Codiolum* is abundant, while in winter and spring *Bangia*, *Ulothrix*, *Hormiscia* and *Enteromorpha minima* replace the *Codiolum*.

6. Because of the almost constant wave action there is an upward displacement of all of these vegetational belts to some 2 or 3 feet above the levels they would occupy on quiet shores, where the distribution of algæ matches average tide-limits, rather than average wave limits.

7. The horizontal zones of vegetation on this shore are often broken

by rills from the tide-pools, which run transversely to the shore line, and thus allow algæ which do not tolerate desiccation to push upward to levels higher than they can attain on exposed rocks. The aspect and algal components of the plant covering of a given rock surface, especially of the upper littoral belt, may differ greatly in different years and even in different seasons of the same year.

8. It has been demonstrated experimentally that *Codiolum* cannot tolerate continuous submergence. *Ascophyllum* does not grow where continuously and completely submerged. Neither alga persists where continuously exposed. Further discussion of the relation of distribution to environment will be published in a later paper.

9. Annual variations in the makeup of the littoral vegetation of the same area have been observed. In August 1925, *e.g.*, barnacles occupied much of the rock surface which had been covered by *Codiolum* during the same month in 1923. *Chondrus* also shows marked annual fluctuations in abundance and distribution.

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DESCRIPTION OF FIGURES¹

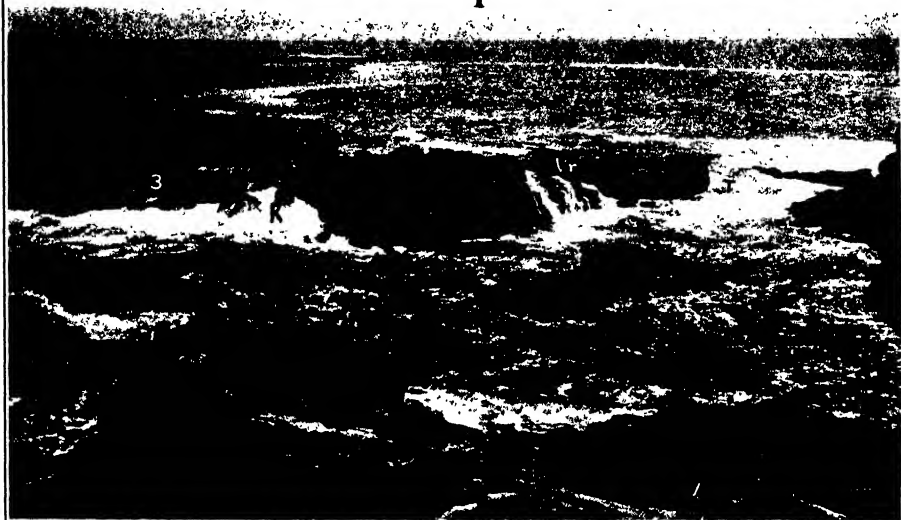
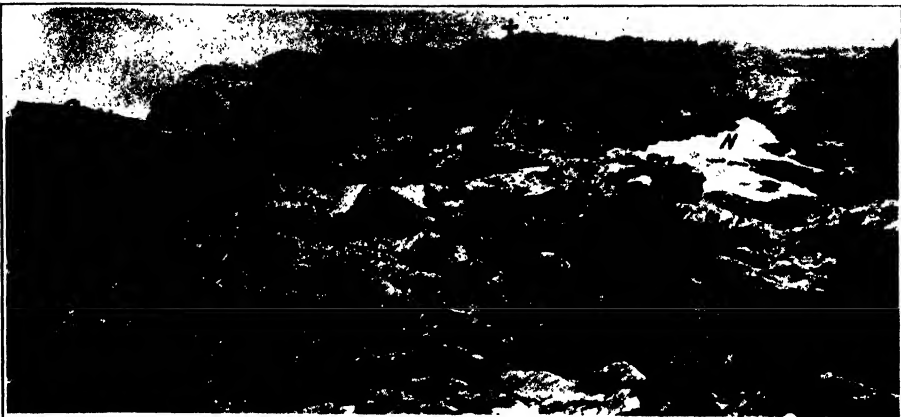
PLATE VIII

FIG. 1. General view of the intertidal portion of the area studied, looking south-east from 50° north by 125° west; bench mark at +; tide stake at S; tide-pools indicated by K, N, and T are those bearing the same letters on the map, Chart II. The numbers 1 to 7 indicate the same rocks in this and in figure 2. Tide at 2 foot level. Photographed July, 1923.

FIG. 2. View of area studied, from 0° north by 100° west, looking east, at high tide; symbols and numbers indicate bench mark, pools and rocks as in figure 1. A short reef and bell buoy in background. Photographed July, 1923.

FIG. 3. Peak of ledge near 90° N. and 40° W. from 6- to 12-foot levels showing contrast in algal covering on shaded and sunlit sides of the same rock. The dark N. W. side, at left, bears a dense stand of *Fucus vesiculosus* (with rarely an *Ascophyllum*)

¹ The photographs are by D. S. Johnson, except figure 19.





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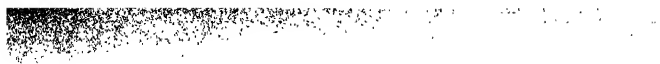
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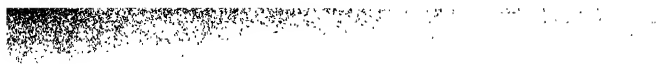
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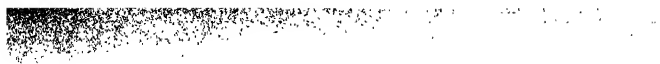
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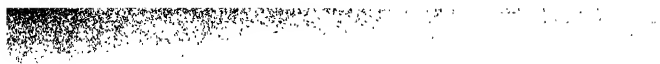
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